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A REVIEW OF THE NORTH AMERICAN TERTIARY SCIURIDAE

By

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With Twenty-Two Plates

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CRAIG C. BLACK

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INTRODUCTION

The family Sciuridae is one of the more cosmopolitan of rodent families, its members occurring in Eurasia, Africa, and North and South America. Tree squirrels, chipmunks, flying squirrels, and a variety of ground squirrels-prairie dogs, marmots, susliks, etc. constitute the family, which is generally divided into two subfamilies: the Petauristinae for the flying squirrels, and the Sciurinae including all other forms. The earliest members are found in the Middle Oligocene of North America and in the Phosphorites (possibly Stampian) of France.

Oligocene and Miocene sciurids have frequently been assigned to the genus *Sciurus*. Such assignments have not been made in the belief that these middle Tertiary species were necessarily referable to *Sciurus* in the strict sense, but rather because the dentition of most members of the family is so conservative that differences between forms are subtle and difficult to detect. Also, much of the material is so fragmentary that its true affinities can only be determined by comparative study of the entire family, living and extinct, a procedure too time consuming to be undertaken in the course of most faunal studies. In Europe, particularly, sciurid specimens have usually been assigned to *Sciurus*, with little or no attention being paid to possible ground squirrel affinities. In North America, on the other hand, specimens referred to most groups of living sciurids have been described, but with the exception of Bryant's work (1945) no attempt has been made to trace the evolution of these groups.

The present study reviews the North American Tertiary members of the family in an endeavor to trace the interrelationships of the known forms. A great deal of sciurid material has been found in various collections which had not previously been studied or even mentioned in the literature. These specimens together with those previously described have provided a much better understanding of the history of the family. Certain generic groups appear to have originated in North America and some of these appear to have been restricted to this continent throughout their history. In the first category are *Marmota,* probably *Eutamias* and possibly *Citellus;* in the second are: *Cynomys, Tamias, Ammospermophilus* and *Tamiasciurus*. As regards *Citellus*, however, such European species as *Sciurus feignouxi*, *Sciurus bredai,* and possibly *Sciurus costatus* resemble spermophiles more closely than they do *Sciurus, S. feignouxi* in particular being very reminiscent of *Miospermophilus*. It is possible, therefore, that the spermophiles had their origin in Eurasia and that the present diversity of ground squirrels in North America is the result of a secondary radiation after immigration. The place of origin of the family and of *Sciurus* itself is unknown.

An adequate understanding of the evolution and distribution of the family can hardly be reached until the Old World Tertiary squirrels have also been studied. Nevertheless, a review of the North American Tertiary representatives should not only serve to elucidate the relationships of these forms but should also supply a basis for an understanding of the record for the family in Europe.

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PREVIOUS STUDIES

For the most part, work on fossil squirrels has consisted of brief treatments of specimens as members of faunas without any serious attempts to arrive at an outline of sciurid evolution. Exceptions to this rule are papers by Bryant (1945) and Wilson (1960); Downs (1956) has briefly discussed many of the known fossil sciurids in connection with a description of *Arctomyoides oregonensis.*

Marsh (1871) was the first to describe a fossil sciurid from the North American Tertiary, placing it in the genus *Arctomys* (=*Marmota*). Cope in 1873 described *Paramys relictus,* which he assigned to *Sciurus* in 1874. With this species, now placed in *Prosciurus,* began the confusion of prosciurines with true squirrels, a confusion that has persisted to the present day. In 1879 and 1881, Cope described two species of *Sciurus, S. ballovianus* and *S. vortmani* from the John Day, both of which are true sciurids. Between 1881 and 1930 the only additions to our knowledge of the North American Sciuridae were Douglass' (1903) account of *Palaearctomys,* the first extinct genus of North American squirrel to be described, Kellogg's (1910) discussion of the Thousand Creek sciurids, Matthew's (1924) brief discussion of *Sciurus aberti* from the Snake Creek, and the description of *Otospermophilus gidleyi* by Merriam, Stock, and Moody (1925). Matthew in 1903 described a specimen from Pipestone Springs as *Sciurus (Prosciurus) vetustus.* In 1910 he raised *Prosciurus* to full generic rank and placed it in the family Ischyromyidae. In this genus he placed Cope's *S. vortmani* and *S. relictus,* leaving only *S. ballovianus* in the Sciuridae. Wood (1937) pointed out that *S. vortmani* was a true sciurid. Since 1937, there has been little confusion as to the proper generic assignment of material either to *Prosciurus* or *Sciurus* but uncertainty still exists as to the position of *Prosciurus* in relation to squirrel evolution, and this will be discussed later (p. 230).

During the 1930's a considerable amount of new material was described, principally by Gazin (1930, 1932) and by Wilson (1936, 1937a) from the Tertiary of the Great Basin. Gazin's contributions included, for the first time, descriptions of fossil spermophiles based on skull material. The first fossil chipmunk was described by Hall (1930) from the late Miocene Barstow Formation.

Matthew (Matthew and Mook, 1933) described a nearly perfect skull from the Deep River Formation, naming it *Sciurus angusticeps,* and took that opportunity to point out that he believed it to be impossible to trace squirrel subgenera into the Tertiary. In particular, he criticized the assignment by Merriam, Stock, and

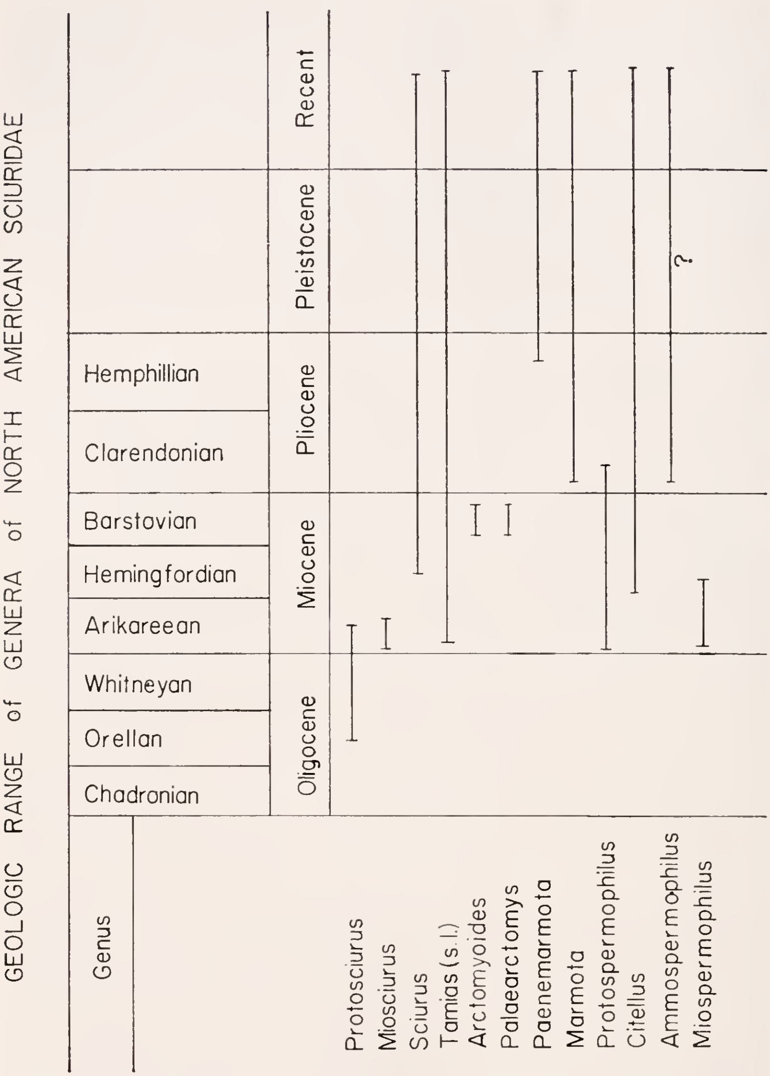
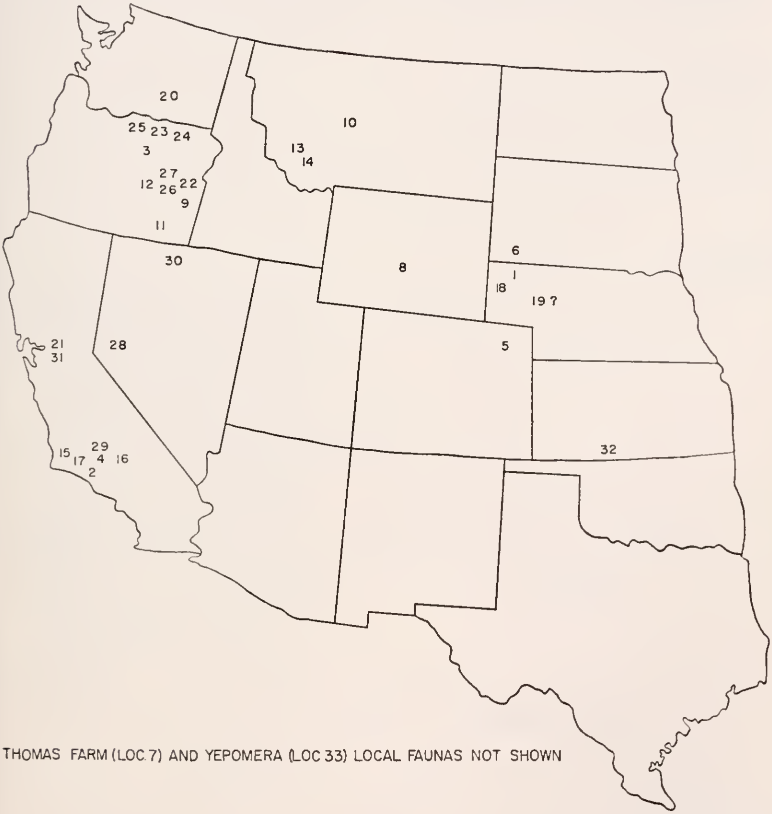


FIGURE 1. Geologic range of all genera of North American sciurids with a pre-Pleistocene fossil record.

Moody (1925) of a mandible from the Rattlesnake to the subgenus *Otospermophilus,* stating that when subgeneric identification could not be made on the basis of a good skull he failed to see how it could be done on a partial ramus.

By the late thirties, a fairly large body of material had been accumulated, including tree squirrels, ground squirrels, chipmunks, and marmots. Bryant (1945), in a work devoted principally to the classification of North American Recent sciurids on the basis of their osteology and myology, discussed for the first time all the known North American fossil squirrels. The broad outlines of sciurid evolution were clarified here and a considerable degree of order brought out of previous uncertainty. However, Bryant



THOMAS FARM (LOC. 7) AND YEPOMERA (LOC 33) LOCAL FAUNAS NOT SHOWN

Figure 2. Geographic distribution of localities from which Tertiary squirrels are known in North America.

did not examine all the pertinent fossil material and his approach, weighted towards the side of Recent species, led to certain misconceptions in his phylogenies. Recently, Wilson (1960) discussed the problems of sciurid evolution in some detail. His discussion of the European material that he was able to examine is especially valuable and he points out for the first time the resemblance of several European late Oligocene and Miocene species to the ground squirrels.

The geologic range of North American sciurids is shown in Figure 1.

The geographic distribution of the material examined for this study is shown in Figure 2. Each locality is represented numerically on the map, with the age of the fauna and the species occurring at that locality listed below.

Oligocene	
Orellan	
1. Meng Ranch, Nebraska	*Protosciurus mengi*
Whitneyan	
2. Las Posas Hills, California	Sciurid indet.
Miocene	
Arikareean	
3. John Day Basin, Oregon	*Miosciurus ballovianus* *Protosciurus condoni* *Protosciurus rachelae* Sciurid indet. (some flying squirrel features) *Protospermophilus vortmani*
4. Tecuya Canyon, California	*Protosciurus tecuyensis*
5. Martin Canyon Quarry A, Colorado	*Miospermophilus bryanti* *Tamias* sp. *Protospermophilus* sp.
6. Wounded Knee local fauna, South Dakota	*Tamias* sp.
7. Thomas Farm l.f., Florida	*Tamias* sp.
Hemingfordian	
8. Split Rock l.f., Wyoming	*Miospermophilus wyomingensis* *Protospermophilus kelloggi* *Tamias* sp.

9. Skull Spring l.f., Oregon	*Protospermophilus malheurensis* *Citellus (Otospermophilus) tephrus*
10. Deep River l.f., Montana	*Protospermophilus angusticeps*
11. Beatty Buttes l.f., Oregon	*Sciurus* sp.
Barstovian	
12. Mascall, Oregon	*Protospermophilus oregonensis*
13. Flint Creek l.f., Montana	*Citellus (O.) primitivus*
14. Lower Madison Valley l.f., Montana	*Citellus (O.) primitivus* *Palaearctomys montanus* *Arctomyoides arctomyoides*
15. Quatal Canyon l.f., California	*Protospermophilus quatalensis*
16. Barstow, California	*Tamias* sp.
liocene	
Clarendonian	
17. Cuyama l.f., California	*Protospermophilus quatalensis*
18. Upper Snake Creek, Nebraska	*Citellus (O.) matthewi*
19. Loup Fork, Nebraska (exact age unknown)	*Citellus (Citellus?)* sp. *Marmota vetus*
20. Ellensburg Beds, Washington	*Citellus (O.) wilsoni*
21. Ingram Creek, California	*Citellus (O.)* sp.
22. Juntura, Oregon	*Ammospermophilus?*
Hemphillian	
23. McKay Reservoir l.f., Oregon	*Citellus (O.) shotwelli* *Citellus (O.) wilsoni* *Citellus (C.) mckayensis*
24. Westend Blowout l.f., Oregon	*Citellus (O.) shotwelli*
25. Arlington Beds, Oregon	*Citellus (O.) wilsoni* *Citellus (O.) shotwelli*

26. Drewsey, Oregon	*Citellus (O.) shotwelli*
27. Rattlesnake, Oregon	*Citellus (O.) gidleyi*
28. Smiths Valley, Nevada	*Citellus (O.) argonautus*
29. Kern River, California	*Citellus (O.) argonautus*
30. Thousand Creek, Nevada	*Citellus (O.) argonautus* *Marmota nevadensis* *Marmota minor*
31. Schell Ranch, California	*Citellus (O.) argonautus*
32. Clark Co., Kansas	*Citellus (O.) fricki*
33. Yepomera l.f., Mexico	*Citellus (O.) pattersoni* *Citellus matachicensis* *Paenemarmota*

METHODS

All measurements are in millimeters and were taken using an ocular micrometer, except those of the skulls and limb bones which were taken with a dial caliper. When two transverse measurements are given for the cheek teeth the first is that across the trigonid, the second across the talonid. Measurements of the teeth were taken across the occlusal surface unless otherwise noted.

The terminology employed throughout is that generally used in the literature dealing with squirrels. The terminology used for the cheek teeth is illustrated in Figure 3.

Tooth structure within the North American Sciuridae falls into two rather distinct categories. M^1-M^2 are subquadrate with expanded protocones, indistinct metaconules and low complete lophs in the tree squirrels, while in the ground squirrels M^1-M^2 are generally triangular with large metaconules, high lophs, and constricted to incomplete metalophs. M_1-M_2 are transversely rectangular to square in the tree squirrels and chipmunks, and they are rhomboidal with narrower lingual than buccal margins in the ground squirrels and marmots. In the first category the posterolophids are low and entoconids generally distinct while in the second the posterolophids are elevated and the entoconids submerged within them.

These two basic types of dentition show various modifications in the North American members of the family but most fossil specimens are easily assignable to one of these groups. Both types

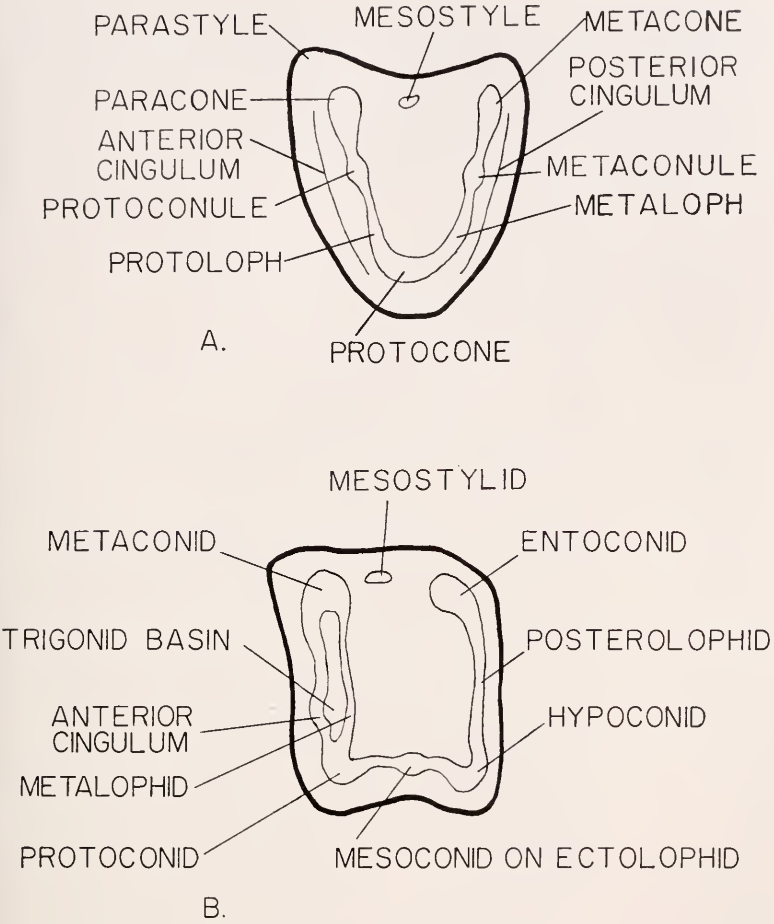


Figure 3. Terminology used to describe occlusal patterns of squirrel cheek teeth. 3a, Upper. 3b, Lower.

are strongly correlated with the two very distinct dietary preferences of the two squirrel groups. The low-crowned heavier dentition of the tree squirrels reflects the primary crushing function of the dentition while the higher-crowned, sharper-lophed dentition of the ground squirrels reflects the greater shearing or cutting action necessitated by the herbaceous diet of this group.

Thanks to the collections of Carnegie Museum and the Museum of Comparative Zoology, specimens of all species of North American Recent Sciuridae have been available for study.

Wood, *et al.* (MS.) has been followed for correlation and terminology of North American deposits.

The following abbreviations are used:

A.C.	Amherst College
A.M.N.H.	American Museum of Natural History
C.M.	Carnegie Museum
C.N.H.M.	Chicago Natural History Museum
F:A.M.	Frick Collections American Museum of Natural History
F.G.S.	Florida Geological Survey
K.U.	University of Kansas Museum of Natural History
L.A.C.M. (C.I.T.)	Los Angeles County Museum (California Institute of Technology Collection)
M.C.Z.	Museum of Comparative Zoology, Harvard University
S.D.S.M.	South Dakota School of Mines and Technology
U.C.M.P.	University of California Museum of Paleontology
U.F.	University of Florida
U.M.M.P.	University of Michigan Museum of Paleontology
U.O.M.N.H.	University of Oregon Museum of Natural History
U.S.N.M.	United States National Museum
U.W.	University of Wyoming
Y.P.M.	Peabody Museum of Natural History, Yale University
a-p	anteroposterior
tr.	transverse
approx.	approximately

CLASSIFICATION

The generally accepted suprageneric classification of squirrels was set forth by Pocock (1923) on the basis of a detailed study of the baculum and glans penis in the family. He recognized six subfamilies within the Sciuridae and separated the flying squirrels as a distinct family. Simpson (1945) accepted Pocock's groupings but reduced his subfamilies to tribal rank and included the flying squirrels in the Sciuridae as a subfamily. Bryant (1945) did not employ formal taxonomic categories above the genus in his classification of Nearctic squirrels, placing related genera in informal divisions and sections, but his classification agreed in most respects with Simpson's modification of Pocock, differing only in that he did not recognize *Tamiasciurus* as tribally distinct from *Sciurus*, and in recognizing *Ammospermophilus* as a distinct genus. Moore (1959), the latest author to revise the Sciurinae, adds two new tribes, Ratufini and Protoxerini, to those admitted by Simpson and transfers *Sciurotamias* from the Callosciurini to the Tamiasciurini.

The classification proposed here differs in two respects from Moore's. First, the chipmunks, *Tamias* and *Eutamias*, are raised to tribal rank and, second, *Tamiasciurus* is included in the tribe Sciurini with *Sciurotamias* returned to the Callosciurini.

Suborder Protrogomorpha
  Family Sciuridae Gray, 1821
    Subfamily Sciurinae Baird, 1857
      Tribe Tamiini new form (Tamiina Moore 1959)
        Tamias, Eutamias
      Tribe Sciurini Burmeister, 1854
        Sciurus, Miosciurus, Protosciurus,
        Tamiasciurus, Reithrosciurus,
        Guerlinguetus, Microsciurus,
        Syntheosciurus, Sciurillus
      Tribe Ratufini Moore, 1959
        Ratufa
      Tribe Protoxerini Moore, 1959
        Protoxerus, Epixerus, Heliosciurus
      Tribe Funambulini Simpson, 1945
        Funambulus, Funisciurus, Paraxerus,
        Myosciurus
      Tribe Callosciurini Simpson, 1945
        Callosciurus, Sundasciurus, Glyphotes,
        Nannosciurus, Dremomys, Lariscus,
        Menetes, Rhinosciurus, Hyosciurus,
        Prosciurillus, Rubrisciurus,
        Exilisciurus, Sciurotamias
      Tribe Marmotini Simpson, 1945
        Citellus, Ammospermophilus, Cynomys
        Marmota, Protospermophilus,
        Miospermophilus, Palaearctomys,
        Arctomyoides, Paenemarmota,
        Paracitellus (?)

Tribe Xerini Simpson, 1945
Xerus, Atlantoxerus, Spermopholopsis
Subfamily Petauristinae Simpson, 1945
Petaurista, Eupetaurus, Sciuropterus,
Glaucomys, Eoglaucomys, Hylopetes,
Aeretes, Trogopterus, Belomys,
Pteromyscus, Petaurillus, Iomys

The tribes Ratufini, Protoxerini, Funambulini, and Callosciurini are retained but I may state that the included genera seem to me to be more closely related to each other and to those of the Sciurini than they are to the Marmotini or to the Xerini. It seems rather unlikely that each group was independently derived from the Tamiini. Unfortunately, there is no paleontological evidence on which to base a tree squirrel phylogeny and I have not had the opportunity to examine representatives of all the Recent genera.

In the following pages I stress the intermediate position of *Tamias* and *Eutamias* between the ground squirrels and the tree squirrels. This is reflected in the skeleton, dentition, and habit. Chipmunks appear to have been a distinct stock since at least the late Oligocene, as have the Marmotini and the Sciurini. Both Bryant (1945) and Moore (1959) recognized that the chipmunks were a distinct group, differing from the marmots, on the one hand, and the spermophiles, on the other, in many cranial and skeletal characters. Bryant set them off as a section within his Terrestrial Squirrel and Chipmunk Division while Moore placed them in a separate subtribe, Tamiina, of the Marmotini. However, I feel that they differ from the marmots and spermophiles as greatly as they do from the tree squirrels and are fully entitled to tribal status.

The tribe Sciurini, as here recognized, includes the European and American tree squirrels plus the North American red squirrel, *Tamiasciurus*. Placement of *Tamiasciurus* in the Sciurini is contrary to majority opinion regarding its relationships. (For a resumé of the taxonomic history of the genus see Moore 1959, pp. 183-184.) Bryant (1945, p. 383) is one of the few recent authorities who has placed *Sciurus* and *Tamiasciurus* together; in most classifications *Tamiasciurus* is given tribal to subfamilial rank, the basis for which is the absence of an os genitale. Layne (1952, 1954) has shown, however, that some individuals do possess vestigial bacula and baubella. The conclusion he reached, namely that reduction of the os genitale is a specialization, is, I believe, valid. Moore (1959, p. 183) concurs but still argues for separate tribal status for *Tamiasciurus*. He emphasizes two skull characters, the presence of three transbullar septa and a high squamosal, that he believes distinguish *Tamiasciurus* from *Sciurus*. However, as he himself points out, some individuals of the Persian tree squirrel *Sciurus (Tenes) anomalus* have three septa, but because this condition is variable in *Tenes* and also because it has a low squamosal, he believes it to be distinct tribally from *Tamiasciurus*. However, the variability in the number of septa in this subgenus of *Sciurus* could argue just as well in the opposite direction. Also, in twenty-six specimens of *Tamiasciurus* examined in the mammal collection of the Museum of Comparative Zoology at Harvard, three showed only two septa, and the third septum was variably developed in the other twenty-three skulls. Perhaps *Tenes* is in the process of acquiring a third transbullar septum, as *Tamiasciurus* may have done in the past; if this is so, the presence of three septa in *Tamiasciurus* need not bar it from close relationship to *Sciurus*. The presence of a low squamosal (a squamosal extending up the side of the skull less than half the distance between the posterior zygomatic root and the postorbital notch) in the Sciurini is a character that is extremely hard to evaluate. What the adaptive significance of this may be is unknown, and a similar uncertainty applies to most of the characters Moore has used. He has set out to find skull characters which would separate groups within the Sciurinae, and, having found a series of characters, he has then defined tribal and subtribal units in terms of them with little or no regard to the relative weight to be given to each character. This is in general the practice followed in keys, which, while allowing for ready identification of individual specimens, all too often obscure actual relationships. However, Moore has managed to convey relationships and natural groupings in most instances, particularly as regards his recognition of the independent origins of the pygmy squirrel groups, but his use of the tribe Tamiasciurini does, I believe, obscure the relationships of this genus. In the majority of its characters *Tamiasciurus* closely resembles *Sciurus*, and its true relationships are, I believe, with that genus.

Moore (1959, p. 183) grouped *Sciurotamias* with *Tamiasciurus* in the tribe Tamiasciurini, again because of the fact that *Sciurotamias* possesses three transbullar septa. He states, however, that in many other skull characters these two genera are quite dissimilar and that this grouping is only tentative. *Sciurotamias* appears to me to be much more closely related to the oriental tree squirrels of the tribe Callosciurini than it is to *Sciurus* and *Tamiasciurus,* and I have placed it in the Callosciurini.

The flying squirrels present serious problems. That they are more closely related to each other than they are to various groups of tree squirrels is, I believe, highly unlikely. *Glaucomys, Sciuropterus, Eoglaucomys* and *Hylopetes* are probably much more closely related to *Sciurus,* and certainly much more closely related to each other, than any of them are to the highly specialized Asian flying squirrels. That the flying squirrels are descended from tree squirrels seems obvious and there is certainly nothing in their morphology that would argue against such derivation. The *Glaucomys* group differs from *Sciurus* in the possession of gliding membranes, in somewhat longer limbs in relation to vertebral column length, and in the wide valley separating the entoconid and metaconid on M_1-M_2. The other forms are generally more specialized, especially in their dentition. From a tree squirrel structural and behavioral base, independent evolution of more than one gliding stock could have occurred. The true relationships of the flying squirrels might best be illustrated by placing some of them in the tribe Sciurini and some in the tribe Callosciurini, possibly as distinct subtribes. However, decision must await a full study of the various Asian genera of flying squirrels and, pending this, I retain the currently recognized subfamily.

The subordinal position of the Sciuridae has been considerably debated in the last decade. Simpson (1945) grouped the squirrels with the Aplodontoidea, Geomyoidea, and Castoroidea in the suborder Sciuromorpha. Wood (1955) removed the Geomyoidea and Castoroidea, split the Aplodontoidea into two superfamilies (Ischyromyoidea and Aplodontoidea transferring the Eomyidae to the Myomorpha) and retained the Sciuroidea within this suborder. Lavocat (1956a), in reviewing recent concepts of rodent classification, suggested that the Sciuridae be placed by themselves in the Sciuromorpha and that the term Protrogomorpha be revived to include the Ischyromyoidea and Aplodontoidea. More recently Wood has proposed (1959), as Lavocat suggested, that either the Sciuromorpha be limited to the Sciuridae and that the Ischyromyoidea and Aplodontoidea be placed in the suborder Protrogomorpha or that the suborder Sciuromorpha be dropped and the Sciuridae remain unallocated to a suborder. Simpson (1959, p. 260) has suggested that all rodents should be either grouped in two suborders, the Caviomorpha and a second suborder for all other rodents, or that no suborders be used in the group and that the classification of the order be extended only to the superfamilial level. Wood (1962, p. 250), in his excellent review of the Paramyidae, follows his earlier (1959) classification and states, "It seems much more appropriate to use the suborder for collections of families large enough to need two levels of superfamilial coordination and to omit suborders for rodents of unknown superfamilial relationship."

I would agree with this statement; however, after a study of the Oligocene and early Miocene squirrels of North America, I believe the Sciuridae should be grouped with Wood's Ischyromyoidea and Aplodontoidea in the suborder Protrogomorpha. As pointed out in detail below, the primitive condition of the zygomasseteric complex in the genera *Protosciurus* and *Miosciurus* bridges the gap between the protrogomorph condition and the fully developed sciuromorph type. In all respects other than zygomasseteric structure, the Sciuridae are much closer to the paramyid evolutionary level than are the Mylagaulidae or Aplodontidae, families which have been placed in the Protrogomorpha because of their primitive zygomasseteric structure. Lavocat (1956a, p. 53) argues that the Sciuridae are only primitive in their dentition while their zygomasseteric complex is specialized. However, they are no more specialized in this respect than the Aplodontoidea are in their dentition. Since early members of both groups can be traced into the Ischyromyoidea, and intermediate stages of zygomasseteric and tooth development are known, it appears much more natural to group the Ischyromyoidea, Aplodontoidea, and Sciuridae together in one suborder. If the Sciuridae were to be considered a separate subordinal group because their zygomasseteric complex is now specialized, the Aplodontoidea should also be given separate subordinal rank because of their dental specializations. This type of fragmentation of natural, closely related groups merely obscures their relationships, however, and I would strongly urge their continued association in one suborder.

Use of the subordinal term Protrogomorpha rather than the older Sciuromorpha for this assemblage is preferable. The sciuromorph type of zygomasseteric structure has been independently evolved in various rodent families, some of which are certainly more closely related to the typical myomorph families than they are to the Aplodontoidea, Ischyromyoidea and Sciuridae, and is thus not diagnostic of a natural group. The suborder Sciuromorpha of Brandt (1855) has changed so completely in recent years that it bears little resemblance to the original. Such families as the Geomyidae, Heteromyidae, and Castoridae, while possessing a sciuromorph type of zygomasseteric structure, are no longer believed to be closely related to the Sciuridae. The Geomyidae and Heteromyidae appear to be myomorphs (see Wilson 1949b) and undoubtedly had an origin within the Paramyidae independent of that of the Sciuridae. The Castoridae were also probably independently evolved from the Paramyidae (Wood, 1955). Since nomenclatural priority is not obligatory in dealing with categories higher than the superfamily, I believe that the use of the subordinal term Protrogomorpha to include the Ischyromyoidea, Aplodontoidea and Sciuridae better expresses our present knowledge of relationships.

SYSTEMATIC REVIEW

Family SCIURIDAE Gray, 1821

Dental formula: I^1_1, C^0_0, P^{1-2}_1, M^3_3. Cheek teeth little advanced over those of the Paramyidae; upper molars triangular to subquadrate with paracone, metacone, protocone as major cusps; no hypocone. M^1-M^2 four crested with conules variably present; posterior cingulum of M^3 enlarged; lower molars rectangular to rhomboidal; entoconids distinct or suppressed in posterolophids; trigonid basins small; masseter coming to extend above infraorbital foramen and onto rostrum with the formation of a flat plate on the anterior surface of the zygoma; infraorbital foramen oval to slit-like.

Range. Middle Oligocene to Recent, North America. Phosphorites to Recent, Europe. Miocene to Recent, Africa and Asia. Recent, South America.

Subfamily SCIURINAE Baird, 1857

The Sciurinae are defined as comprising that group of sciurids lacking gliding membranes.

Range. Middle Oligocene to Recent in North America.

Tribe TAMIINI new rank (Tamiina Moore 1959)

Limbs intermediate in proportion between Marmotini and Sciurini; three sacral vertebrae; skull moderately convex; infraorbital foramen oval, no infraorbital canal; diastema long; diastemal part of mandible drops only slightly anterior to P_4; upper molars subquadrate; metaconules small; metalophs only slightly constricted at protocones; entoconids incorporated into posterolophids; posterointernal corner of M_1-M_2 angular; M_1-M_2 not compressed anteroposteriorly.

Range. Early Miocene to Recent in North America.

TAMIAS Illiger

Type species. Sciurus striatus Linnaeus

Except on characters of the baculum and upper dentitions which show the presence or absence of P^3, it is impossible to distinguish *Eutamias* from *Tamias*. None of the material described below, therefore, can be placed in one genus of chipmunk rather than the other with any certainty. The material is much too fragmentary to warrant erection of a new genus and has consequently been placed in *Tamias* as a purely arbitrary assignment. However, this has not been done with any belief that these specimens truly represent species of the Recent genus.

TAMIAS sp.

Plate 1, figure 1

Referred specimens. S.D.S.M. Nos. 58100-26 LP^4, 58100-25 $RM^{1\text{ or }2}$, 58100-29 $RM^{1\text{ or }2}$, 58100-31 $RM^{1\text{ or }2}$, 58100-28 LM^3, 58100-32 LdP^4, 58100-3 RP_4, 58100-2 $LM_{1\text{ or }2}$.

Horizon and locality. Sharps formation, Lower Arikareean, early Miocene. Wounded Knee local fauna, Pennington County, South Dakota.

Description. The deciduous fourth upper premolar is triangular in outline with a narrow protocone and expanded anterior cingulum. The lophs are complete, rather high, and each shows the presence of a conule. The mesostyle is large; the posterior cingulum reduced. P^4 is worn and somewhat broken along its buccal margin. In outline the tooth is nearly rectangular due to a large protocone and small anterior cingulum. The protoloph is complete and shows no sign of a protoconule; the metaloph is partially constricted and bears a prominent metaconule. The mesostyle and posterior cingulum are small. There are three teeth that are either first or second upper molars. One, S.D.S.M. No. 58100-25, appears to be somewhat squarer in outline than the other two but this is at least partially due to its increased stage of wear. S.D.S.M. No. 58100-31 differs from the other two in having a distinct protoconule and metaconule. All three teeth are otherwise similar in crown pattern. The protocone does not occupy the entire lingual margin but is larger than in the Recent species. As a result the teeth are more nearly square than they are in living forms. This squareness is also contributed to by a rather expanded and angular protocone-posterior cingulum crest. The lophs are complete, relatively low, and show no signs of conules in Nos. 58100-25 and 58100-29. The mesostyle is well developed. M^3 is only slightly larger than M^1 or M^2 and is triangular in outline. It is not greatly expanded posteriorly. There is a faint indication of a metaloph remnant passing from the base of the protocone into the central basin. The protoloph is low, and no mesostyle is present. The protoconid and metaconid of P_4 are very closely appressed and there is no indication either of an anteroconid or of a trigonid basin. The buccal valley is very broad and shallow. The entoconid is submerged in the high posterolophid. The mesostylid is large. $M_{1 \text{ or } 2}$ is as long as it is wide. There is no trace of an anteroconid. The entoconid is distinct and the entoconid corner angular. A large mesoconid fills the broad shallow buccal valley. Although the tooth is worn, the posterolophid does not appear to have been high.

Discussion. The eight teeth in this collection and the other isolated teeth assigned below to the Tamiini resemble those of *Tamias ateles* Hall more closely than they do any other sciurid teeth from the North American Tertiary. In fact it is quite remarkable how little difference exists between these early Miocene forms and those from the Barstow and Tonopah. The upper molars agree with those from the Martin Canyon Quarry A in Colorado and the Barstow material in being rather square in outline and in having low lophs with no indication of protoconules. Large mesostyles are present in the upper molars of the Wounded Knee specimens and on those from Barstow. The partial constriction of the metaloph and development of a metaconule are not seen until the Barstovian *Tamias ateles* stage is reached with the exception of one tooth in the Wounded Knee fauna, S.D.S.M. No. 58100-31. The lower molars also are extremely similar for all the Miocene specimens known. The rather low posterolophid of the South Dakota *Tamias* specimens is an ideal starting point for the development of the higher posterolophids seen in the later forms.

TAMIAS sp.

Plate 1, figure 2

Sciurus sp. B Wilson, 1960, p. 63.

Referred specimens. K.U. No. 10170 $LM^{1 \text{ or } 2}$, 10171 RM^3, 10172 $RM_{1 \text{ or } 2}$.

Horizon and locality. Pawnee Creek Formation, Upper Arikareean, early Miocene. Martin Canyon Quarry A, NW ¼, Section 27, T.11N., R.53W., Logan County, Colorado.

Description. The first or second upper molar is square with a rather small protocone situated in the middle of the lingual border and a small cusp-like expansion at the junction of the posterior cingulum with the protocone. There is no indication of a mesostyle and there is no large parastyle at the buccal termination of the anterior cingulum. The lophs are low and there is no indication of either a protoconule or metaconule. M^3 is well worn. It is triangular in occlusal outline with no marked posterointernal expansion. The lower molar, although larger and somewhat more compressed anteroposteriorly, resembles that from the Lower Hemingfordian Split Rock local fauna. There is a strong anteroconid on the anterior cingulum. The trigonid basin is extremely small and opens into the talonid basin with only a weak metalophid present. The posterolophid is high with the entoconid submerged within it. The buccal valley is deep and tapers internally. There is no trace of a mesoconid and the ectolophid is weak. A small mesostylid is present.

Discussion. These *Tamias* specimens from Colorado differ from the Wounded Knee specimens but agree with all other Miocene chipmunks in lacking the mesoconid and could easily have been ancestral to the later forms. Likewise, they could have been derived from the older Wounded Knee population through a loss of the mesoconid and elevation of the posterolophid.

TAMIAS sp.

Plate 1, figure 3

Black, 1963, p. 487.

Referred specimens. F.G.S. V-6021, $LM^{1 \text{ or } 2}$, F.G.S. V-6020, RP_4, U.F. No. 3873, a fragment of left mandible with M_1 and F.G.S. No. V-5951, RM_3.

Horizon and locality. Arikareean, early Miocene. Thomas Farm, Gilchrist County, Florida.

Description. The following description is quoted from Black, 1963 (pp. 487-488). "The upper molar is unworn and shows a high, somewhat compressed protocone. The anterior cingulum is broad and joins the protocone at its base, well below the level of the protoloph. Buccally, the anterior cingulum bears a small parastyle. The protoloph and metaloph are low and complete, merging with the protocone about halfway down its buccal slope. A small metaconule is present in the metaloph. The posterior cingulum is narrow but expands slightly where it joins the protocone. A small mesostyle is present at the base of the paracone.

"The diastema of the mandible is long in relation to overall size and the diastemal depression shallow. P_4 has a trapezoidal shape with the protoconid and metaconid separated by a narrow notch. There is no indication of an anterior cingulum or anteroconid. The posterolophid is somewhat elevated and passes in a gentle curve from the hypoconid to the entoconid with the entoconid submerged within the posterolophid. There is no mesostylid present. The ectolophid is low and weak and bears no trace of a mesoconid. M_1 is square in outline with an angular entoconid corner. A small anteroconid is present on the anterior cingulum. The metalophid is complete and the small trigonid basin completely enclosed. The posterolophid is low. The entoconid is submerged in the posterolophid. The ectolophid is low and weak and the buccal valley is shallow. No mesostylid is present. The M_3 is extremely elongate, more so than in any other sciurid and it is quite possible that this is not a chipmunk M_3 and should not be associated with the other material described here. However, the tooth bears no resemblance to that of the prosciurines and on the basis of size alone it is here tentatively referred to *Tamias*. Most of the enamel on the tooth is missing and the crown pattern obliterated."

Discussion. These specimens represent the only Tertiary record for the family east of the Mississippi. Future work at Thomas Farm will undoubtedly bring to light more material of this species but, until then, little can be said about the relationships of this sciurid. The material available, with the exception of M_3, agrees well with the chipmunks known from the Miocene of South Dakota, Wyoming, and Colorado, and it probably belongs with this group. In size, this population is closer to the Split Rock *Tamias* than to the earlier South Dakota and Colorado populations.

TAMIAS sp.

Plate 2, figure 1

Referred specimen. U.W. No. 1434 $LM_{1 \text{ or } 2}$.

Horizon and locality. Split Rock Formation, early Hemingfordian, middle Miocene. NW ¼, Section 36, T.29N., R.90W., Fremont County, Wyoming.

Description. The molar is square in occlusal outline and smaller than that of *Tamias ateles* Hall. There is a large anteroconid closing the trigonid basin anteriorly but the basin is open posteriorly as the metalophid is incomplete. The buccal valley is deep and there is no mesoconid present. The entoconid is submerged in the high posterolophid. There is no mesostylid.

Discussion. This is one of the smallest sciurids known from the North American Tertiary. It resembles the other specimens herein described as members of the Tamiini in all respects and is closer in size to the Thomas Farm chipmunks than to the other Miocene forms.

TAMIAS ATELES (Hall)

Plate 2, figure 2

Eutamias ateles Hall, 1930, p. 314; Wilson, 1942, p. 104.
Tamias (Neotamias) ateles Bryant, 1945, p. 358.

Type. U.C.M.P. No. 28521, RM^1-M^3.

Hypodigm. Type and U.C.M.P. Nos. 28522 RM^1, 28523 RM_3, L.A.C.M. (C.I.T.) No. 5236a $RM_{1 \text{ or } 2}$, No. 5236b $LM_{1 \text{ or } 2}$, No. 5236c $LM^{1 \text{ or } 2}$.

Horizon and locality. Barstovian, late Miocene to Clarendonian, early Pliocene. Eleven miles N.E. of Hinkley, San Bernardino County, California. Also C.I.T. Loc. No. 172, 9 miles N. of Tonopah, Nevada.

Emended diagnosis. Teeth small; protoconules absent; protolophs not constricted at junction with protocone; metaconules present; mesostyles large; posterointernal part of M_3 large; talonid basin enclosed by high narrow posterolophid and lingual lophid; entoconid not distinct; no mesoconid.

Description. M^1 and M^2 are rather square in occlusal outline, more so than in Recent *Tamias,* due to the greater expansion of the lingual end of the posterior cingulum. The anterior cingula are moderately enlarged but there is no prominent parastyle. The lophs are low and resemble those of living *Tamias* in absence of a protoconule, presence of a metaconule, and partial constriction of the metaloph at the protocone. The mesostyles are large, whereas in Recent species they are small and indistinct, blending into the posterior base of the protocone. M_3 differs from its counterpart in Recent species only in the retention of a vestigial metaconule. In outline, the tooth is broadly triangular with little or no constriction of the posteroexternal portion.

Discussion. As has already been discussed, *Eutamias ateles* is extremely similar to the early Miocene forms known from the Great Plains and could have easily evolved from the Colorado population. Although slightly larger, *T. ateles* is also nearly identical to the Recent *Tamias striatus* and *Eutamias minimus*. The slight constriction of the metaloph and the absence of the mesoconid agree well with these species. However, *T. ateles* agrees almost equally well with other living species and it is certainly much too early in time to be conspecific with any of the Recent forms.

Measurements of *Tamias* sp.

		Wounded Knee l.f.	Martin Canyon l.f.	Thomas Farm l.f.	Split Rock l.f.	Barstow	Tonopah
dP^4	a-p	1.3					
	tr.	1.4					
P^4	a-p	1.3					
	tr.	1.5					
$M^{1 \text{ or } 2}$							
	a-p	1.3, 1.4, 1.3	1.7	1.3		1.3, 1.4, 1.5	1.4
	tr.	1.6, 1.7	1.9	1.5		1.6, 1.6, 1.7	1.6
M^3	a-p	1.5	1.7			1.6	
	tr.	1.6	1.7			1.6	
P_4	a-p	1.4		1.2			
	tr.	1.2–1.4		1.0–1.2			
$M_{1 \text{ or } 2}$							
	a-p	1.3	1.7	1.2	1.2		1.4, 1.5
	tr.	1.3–1.4	1.6–1.7	1.2–1.2	1.1–1.1		1.5–1.6, 1.5–1.5
M_3	a-p			1.8			
				1.4–1.3			

Tribe Sciurini Burmeister, 1854

Limbs long, slender; distal ends of radius and ulna, and tibia and fibula slender; three sacral vertebrae; skull roof convex, more so than in the Marmotini (except in *Protosciurus* and *Miosciurus*); zygomatic plate inclined at 60° or more in relation to basicranial axis; skull broad interorbitally; diastema short and diastemal part of mandible drops steeply anterior to P_4 (except in *Miosciurus*); anterior end of mandible below level of alveolar border; upper molars quadrate with protocone occupying most of lingual border; metaconules small to absent; lophs low; entoconids generally large and distinct; posterolophids low.

Range. Middle Oligocene to Recent in North America.

MIOSCIURUS n. gen.

Type species. Sciurus ballovianus Cope.

Diagnosis. Size small; skull narrow, skull roof flat; cranium deeper than in *Protosciurus;* zygomatic plate triangular, facing anterolaterally, bounded by distinct anterior and dorsal ridges; diastema short, very shallow; mental foramen high on side of jaw; masseteric fossa ending below M_1; teeth low crowned; lophs low on upper molars; conules absent; entoconids and anteroconids distinct.

Range. Early Miocene, John Day Basin, Oregon.

Miosciurus resembles *Protosciurus* and *Sciurus* in possessing low-crowned cheek teeth, large protocones, low lophs on the upper molars and square lower molars with distinct entoconids. However, it is easily distinguished from *Sciurus* by the absence of a well-developed sciuromorph masseteric complex. The masseter is restricted to the anterior and lateral portions of the zygomatic arch and had not yet migrated forward beyond the infraorbital foramen onto the rostrum. In keeping with the primitive condition of the zygomatic plate, the masseteric fossa ends below M_1 not yet having migrated forward under P_4. *Miosciurus* is distinguished from *Protosciurus* by its smaller size, relatively deeper cranium in relation to skull width, shallow diastemal depression and more superior position of the mental foramen. In general, the lower molars tend to be somewhat shorter in relation to their width than they do in *Protosciurus* and the posterior cingulum-protocone union is not as expanded as in that genus. As will be discussed later, it appears likely that *Miosciurus* is close to the point of the ground squirrel divergence.

MIOSCIURUS BALLOVIANUS (Cope)

Plate 2, figure 3

Sciurus ballovianus Cope, 1881, p. 177.

Type. A.M.N.H. No. 6901, incomplete skull, both mandibles, and the head of the right humerus.

Hypodigm. Type only.

Horizon and locality. *Diceratherium* Beds, John Day Formation, early Miocene. John Day Basin, Oregon.

Diagnosis. As for genus.

Description. The rostrum is short and was probably somewhat deeper than long. Bryant (1945, p. 345) states that it is narrow but this is apparent only and undoubtedly due to displacement of the right premaxilla towards the midline. It must in fact have been rather broad in relation to the overall size of the skull. The frontal projections of the premaxillae are broad, as in *Sciurus* and *Tamias*. A major portion of both the frontals and parietals is missing, exposing casts of the olfactory lobes and the cerebrum. A thin rim of bone is left along the upper border of the orbits with the postorbital process preserved on the left side; it is long and slender, tapering to a thin point and is directed outward, backward and downward. The interorbital distance is relatively great, as in tree squirrels, and the skull roof is flat.

In the construction of the zygomatic plate *Miosciurus ballovianus* resembles some species of *Protosciurus*. The plate is triangularly shaped, bordered by rather well-developed ridges, and faces downward, forward, and outward. It lies lateral and dorsal to the infraorbital foramen but does not expand beyond it onto the rostrum. The masseteric tubercle is small and lies at the lateroventral margin of the oval infraorbital foramen. The infraorbital foramen is situated a short distance anterior to P^3; it is more ovate than is indicated by Bryant's description. The zygomatic notch would appear to have been opposite P^4-M^1 although this is difficult to determine since these teeth are missing on the right side and the alveoli are broken. There is no indication that any part of the masseter spread onto the premaxilla, and there is no trace of a pouch muscle pit behind the incisors. The palate is much too broken and distorted to provide any information.

Both mandibles lack the coronoid, condyle, and angle. The diastema is short and the diastemal depression shallow with the mental foramen lying near its dorsal border just anterior to P_4. The masseteric fossa is rounded and ends below the posterior end of M_1. The ascending ramus arises opposite the middle of M_3.

The upper incisors are oval in cross section and are wider and not as deep as those of the living sciurids. Of the upper cheek teeth only the left M^1 and right M^2 are preserved; the alveoli show that P^3 was present. Both molars are subquadrate with enlarged protocones, but these are not as broad as in *Protosciurus* and *Sciurus*. The protocones are sharper cusps and the posterior cingulum is not expanded at the protocone as in those genera. Protolophs and metalophs are complete, directed somewhat anteriorly, and show no indication of conules. The anterior cingulum is large and rises to a high parastyle; the posterior cingulum is much smaller and fuses with the posterior slope of the metacone before reaching the buccal margin. The mesostyles are large.

The lower incisors are not as compressed as in the Recent squirrels, and are somewhat more convex buccally. The molars increase in size from M_1 to M_3. The trigonids are much higher than the talonids. M_1 and M_2 are rather square with large entoconids and rounded entoconid corners. The anteroconid of M_1 is large and only slightly constricted at its union with the protoconid. On M_2, however, there is a furrow between the anteroconid and protoconid on the buccal face of the tooth and the anteroconid-protoconid union is greatly constricted. The metalophid is complete on both M_1 and M_2 although stronger on M_1, and the trigonid basins are small. The buccal valleys are broad and dammed by weak ectolophids. The hypoconids are somewhat larger than the protoconids. M_3 is similar in most details except that the hypoconid is much larger than on the other molars. The tooth has the typical, rather elongate sciurid shape, and there is an expanded, blade-like posterolophid.

Discussion. *Miosciurus ballovianus* appears to stand in an intermediate position between the chipmunks, on the one hand, and the tree squirrels, on the other. It resembles tree squirrels in: (1) low-crowned, rather heavy dentition; (2) low protolophs and metalophs; and (3) absence of metaconules. *M. ballovianus* resembles chipmunks in: (1) deep cranium; and (2) slight drop of mandible anterior to P_4. In several characters such as the slightly constricted and sharp protocone, the elevated posterolophid, and the partially submerged entoconid, it is intermediate between these two groups but somewhat more chipmunk-like than tree squirrel-like.

This combination of characters leads me to believe that *M. ballovianus* is not far removed from the point of tree squirrel-ground squirrel divergence and that most of the characters seen in this species were present in the ancestor of these two groups.

The shallow diastemal depression, primitive masseteric complex, slightly constricted protocone, and the condition of the entoconid are all characters which were probably present in the ancestral population. However, the deep cranium and complete absence of metaconules would rule out *M. ballovianus* as the ancestor for both tree squirrels and ground squirrels. It does not appear to have left any descendants but it cannot be far removed from the major point of divergence in sciurid evolution.

Measurements

Interorbital width	approx.	7.5
Depth of diastema at mental foramen		3.1
Depth of mandible below M_1		4.2
Length of diastema	approx.	2.7

	a-p	tr.
RI^1	1.6	1.0
LI^1	1.6	1.0
LM^1	1.5	1.7
RM^2	1.5	1.7
RI_1	0.9	1.8
LI_1	0.9	1.8
LM_1	1.5	--- -1.5
LM_2	1.6	1.6-1.6
LM_3	1.8	1.7-1.5
RM_1	1.5	1.5-1.5

PROTOSCIURUS n. gen.

Type species. Protosciurus condoni n. sp.

Diagnosis. Skull roof flat; cranium broad, shallow; masseter restricted to masseteric tubercle and lateral margin of zygoma, not passing over the infraorbital foramen onto the rostrum; masseteric fossa ending below M_1; diastema short; diastemal depression deep; mental foramen considerably below level of diastema; cheek teeth low crowned; lophs on upper molars low; conules reduced or absent; entoconids large on lower molars; buccal valley wide, shallow.

Range. Middle Oligocene of Nebraska, late Oligocene or early Miocene of Oregon, early Miocene of California.

Discussion. Protosciurus condoni, the type species, is based on an excellent skull that affords a good understanding of the genus. The mid-Oligocene *P. mengi* may confidently be grouped with it, but the remaining species are placed here primarily as a matter of convenience pending better knowledge of them. They agree with *P. condoni* in having cheek teeth of tree squirrel type combined with at least some indication that the zygomasseteric structure had not yet attained the complete sciuromorph condition. It is possible that certain of the European Oligocene and early Miocene forms should be included with this group. However, until all the European material can be adequately reviewed, I restrict *Protosciurus* to the North American forms.

PROTOSCIURUS CONDONI[1] n. sp.

Plates 3, 4

Type. U.O.M.N.H. F-5171, nearly complete skull lacking only the zygomatic arches and rostrum anterior to the incisive foramina and the right mandible lacking the incisor and angle.

Hypodigm. Type only.

Horizon and locality. John Day Formation, Oregon. (The specimen was collected by Condon in 1870 and no further locality data were given.) Late Oligocene or, more probably, early Miocene.

Diagnosis. Largest species of genus; masseteric fossa deep, ending below middle of M_1 with no muscle scar anterior to it; deep pit for insertion of *M. temporalis* behind M_3; protoconules minute on M^1-M^2, metaconules present; M_1-$_2$ not as long in relation to width as in *P. tecuyensis;* no mesoconids.

Description. The skull is extremely flat dorsally, curving only slightly from a point above the posterior root of the zygoma to the occiput. It is broad interorbitally with no supraorbital notch, shallow at the orbits, and little inflated in the cranium. The rostrum is broad but not deep. The origin of the postorbital process is broad and the process itself is drawn out to a fine point. The lyre-shaped temporal ridges are very weak, originating at the posterior end of the postorbital processes and meeting in a rather stout sagittal crest some little distance in front of the occiput.

The nasals are slender posteriorly, where they project well behind the premaxillary-frontal suture. The premaxillae are broadly expanded at their suture with the frontals and almost exclude the maxillae from the dorsal surface of the rostrum. The premaxillary-maxillary suture on the side of the rostrum is vertical. There is no indication of any swelling of the premaxillae

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[1] Named for the late Professor Thomas Condon in recognition of his pioneering work in the John Day Basin.

lateral to the incisors such as is seen in the protospermophiles. Unfortunately, the extent of the participation of the maxillae in the formation of the anterior root of the zygoma cannot be determined. There is no indication that the masseter had expanded anterior to the infraorbital foramen; it appears to have been confined to the zygomatic root lateral to the infraorbital foramen and to the masseteric tubercle. The portion of the zygomatic plate preserved does not exhibit the anterolateral torsion seen in *Miosciurus*. The zygomatic notch is opposite the posterior end of P_4. The masseteric tubercle is large and lies below and lateral to the infraorbital foramen. The infraorbital foramen opens just anterior to, and slightly above P^3. It is ovate, expanded at the bottom and compressed at the top. The canal is moderately long.

As in *Marmota* and *Sciurus*, the tooth rows are parallel and the palate is broad. The posterior palatine foramen lies opposite the anterior end of M^3 and just behind the maxillary-palatine suture rather than on it. The internal narial opening is broad and does not pinch in posteriorly as in the spermophiles. The pterygoid fossa is narrow but very deep and is bounded laterally by a well-defined ectopterygoid ridge, which, although partially broken in this specimen, was clearly higher and stouter than in Recent squirrels. The pterygoid plate is broad and probably extended back to the bulla.

The ventral wing of the alisphenoid is in contact with the palatine and the pterygoid with a single foramen, the fused buccinator and masticatory, lying in the center of the wing. The alisphenoid turns upwards and slightly backwards just behind the foramen ovale. There is no sharp notch formed between the alisphenoid and bulla as is seen in *Cedromus*. The foramen ovale lies immediately behind the pterygoid fossa with a foramen medial to the foramen ovale for a vein connecting the internal maxillary veins. There appear to be two foramina situated posterior and medial to the foramen ovale, one of which may be the foramen lacerum medium and the other the eustachian canal. The dorsal wing of the alisphenoid cannot be traced with any certainty but it does not appear to pass as far dorsally in the posterior wall of the orbit as it does in modern squirrels.

The exact limits of the bones within the orbit cannot be seen on this specimen. The sphenopalatine foramen would appear to be bounded above by the frontal, anteriorly and below by the maxilla and posteriorly by the orbital process of the palatine. A small sphenofrontal foramen is present as in *Sciurus*. The posterior wall of the orbit is flat rather than gently rounded and the internal limit of the orbit narrows to a very deep groove. The large optic foramen opens into this narrow area and just below and behind the optic foramen the sphenoidal fissure opens into the orbit.

The squamosal forms a greater part of the posterior wall of the orbit than it does in *Sciurus* or *Marmota,* passing over the optic foramen and almost reaching the medial wall. Dorsally the squamosal almost reaches the postorbital notch. Immediately behind the posterior zygomatic root, a distinct postglenoid foramen is present.

The lateral margins of the basioccipital are prominently raised, buttressing the bullae medially, and these ridges are carried forward on the basisphenoid to just behind and medial to the foramen ovale. The basioccipital is quite broad and extends forward to meet the basisphenoid well behind the foramen ovale as in *Sciurus* and *Marmota,* but in contrast to *Paramys* (Wood, 1962, p. 17) where the suture lies at the posterior margin of the foramen. There is no prominent median heel on the basioccipital but there is a wide, shallow arch running forward along the midline of the bone. The foramen lacerum posterius is large, more so than in Recent sciurids, and lies between the petrosal and basioccipital at the posteromedian angle of the bulla. Just posterior to the foramen lacerum posterius a single hypoglossal foramen passes through the basioccipital. The bullae are compressed laterally and hence appear more elongate than in Recent forms; two and a half transbullar septa are present. The occiput is broad and shallow, sloping only slightly posteriorly. The paroccipital processes are broken but appear to have been large. Just above them the occiput is more deeply concave than in the modern forms. The foramen magnum and condyle are as in *Sciurus.*

The mandible is heavy with a deep and relatively short diastema. The mental foramen lies below the diastemal level and only a short distance anterior to P_4. The masseteric fossa is deep and set off by heavy ridges above and below; it extends forward to the back of M_1 with no indication of a scar anterior to this point. The condyle is elongate anteroposteriorly and faces upward and slightly outward. The coronoid process rises from a broad base and curves upward and backward, but the dorsal border does not become horizontal as it does in *Citellus.* Immediately behind M_3 and internal to the ascending ramus there is a deep pit for the insertion of *M. temporalis,* which suggests a much greater development of this muscle especially of its medial part in *Protosciurus,* than in Recent forms. This, together with the deep pterygoid fossa, accords with the fact that the masseter complex was not yet fully developed into the sciuromorph type. With the exception of this pit and the posterior position of the masseteric fossa the mandible closely resembles that of *Sciurus carolinensis.*

P^3 is a stout peg. P^4, although somewhat smaller than M^1-M^2, is completely molariform, resembling M^1-M^2 in all details. These three teeth are all broad internally with a large protocone and expanded protocone-posterior cingulum crest within which a small cusp is evident. The anterior cingulum is large but there is no well developed parastyle. The lophs are low, complete, and show small protoconules and metaconules. The buccal border is preserved only on the left M^2. Here a small mesostyle is present at the base of the paracone. M^3 is the largest tooth in the series with a greatly expanded metacone. There is no sharp indentation between protocone and metacone; the posterior cingulum passes evenly posterointernally from the protocone to the metacone.

P_4 is badly broken, but it would appear that the protoconid and metaconid were closely appressed; it is impossible to determine whether or not an anteroconid was present. M_1 and M_2 are nearly square in outline. The four principal cusps are large, and there are well developed anterior cingula and mesostylids present, but there is no sign of a mesoconid. The buccal valleys are broad, rather shallow, and slope from the talonid basin to the buccal margin. The entoconid corners are angular and the posterolophids low. M_3 is the largest tooth of the series. It displays a prominent anteroconid, a mesostylid, an expanded entoconid, and a very large hypoconid. The posterior half of the tooth is almost as wide as the anterior half, a condition generally true for Recent tree squirrels and chipmunks but not for other members of the family.

Discussion. P. condoni, while decidedly primitive, is certainly a tree squirrel and an almost ideal ancestor for the later tree squirrels. With an increase in depth of the cranium, a greater flexure of the basicranial axis (probably in conjunction with increased arboreal activity), further perfection of the zygomasseteric structure, and minor changes in the dentition, *P. condoni* could readily be transformed into *Sciurus.* However, due to the scarcity of tree squirrels in the fossil record this transition cannot be documented at present, but it probably took place through a stage such as is represented by *P. rachelae* also from the John Day. *P. condoni* is clearly distinct from *Cedromus* or *Prosciurus* but unfortunately tells us little about the possible paramyid ancestry of the family. As stated elsewhere (p. 230), I do not believe *Cedromus* to be a sciurid or to have had any direct connection with the ancestry of the family.

Measurements

Interorbital width at supraorbital notch	23.0
Interorbital width at postorbital notch	19.0
Depth rostrum anterior to masseteric tubercle	16.2
Depth cranium behind M^3	19.4
Depth cranium at anterior end of bullae	19.2
Width across occiput	30.5
Length of diastema	9.9
Length of mandible, anterior tip to condyle	47.1
Alveolar length P^3-M^3	15.8
Alveolar length P_4-M_3	14.9

PROTOSCIURUS MENGI[1] n. sp.

Plate 5, figure 1

Type. U.M.M.P. No. 39559, portion of left horizontal ramus with P_4-M_3.

Hypodigm. Type only.

Horizon and locality. Lower Orellan, Middle Oligocene. A. Meng Ranch, S.12, T.33N., R.54W., northwest of Crawford, Sioux County, Nebraska.

Diagnosis. Smaller than *P. condoni;* M_{1-2} not as long in relation to width as in *P. tecuyensis;* mesoconids strong.

Description. The masseteric fossa appears to have terminated below M_1 but the mandible is too badly broken to be absolutely certain of this. The origin of the ascending ramus is at the posterior border of M_2. There is a pit behind M_3 for the insertion of part of *M. temporalis.*

The teeth increase in size from P_4 to M_3. Strong entoconids, mesostylids and mesoconids are present on all the teeth. The anteroconid is a distinct cusp on P_4 but blends progressively into the anterior cingulum on M_1-M_3. The trigonid is considerably higher than the talonid. The metalophid is progressively weaker from P_4-M_3 and the trigonid basin is small on all teeth. The entoconid is large and distinct but partially incorporated in the posterolophid which is higher than in *Sciurus* or *Protosciurus condoni.* The entoconid corner is very slightly rounded. The mesoconid slopes buccally on all the teeth leaving little or no shelf area in the buccal valley. The enamel of the talonid basin is finely wrinkled on all teeth.

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[1] Named for A. Meng on whose ranch the specimen was collected.

Discussion. *P. mengi* is the oldest known sciurid. It resembles Recent tree squirrels in many respects and seems certainly to belong with that group of sciurids. However, its dentition differs from that of *Sciurus* in the following characters: (1) The teeth are not as wide as those of *Sciurus;* (2) the posterolophid is somewhat higher thus submerging more of the entoconid within it; (3) the trigonid is higher; and (4) the metalophid is weaker. *P. mengi* agrees with *P. condoni* as regards the first of these characters but differs from *P. condoni* as regards the other three. *P. mengi* bears some resemblance to *Sciurus* sp. (Stehlin and Schaub, 1951, p. 198, fig. 295 A) from the upper Stampian. However, the trigonid basin and entoconid are smaller in *P. mengi* and the metalophid is not as strong.

As one would expect, the characters seen in *P. mengi* are neither those of a typical tree squirrel nor ground squirrel but are intermediate between these two groups in most respects. With an increased development of the posterolophid and incorporation of the entoconid within it, *P. mengi* could easily have given rise to the small chipmunk-like sciurids of the early Miocene and through this stage to the *Miospermophilus* ground squirrels. Likewise, *P. mengi* is very probably close to the ancestry of *P. condoni* and possibly other members of the genus.

Measurements

Alveolar length P_4-M_3	11.4

PROTOSCIURUS TECUYENSIS (Bryant)

Plate 5, figure 2

Sciurid sp. Stock, 1920, p. 272.
Sciurus tecuyensis Bryant, 1945, p. 341.

Type. U.C.M.P. No. 23611, partial right mandible with M_1-M_2.

Hypodigm. Type only.

Horizon and locality. Lower Arikareean, early Miocene. East side Tecuya Canyon, about 35 miles south of Bakersfield, Kern County, California.

Emended diagnosis. Jaw heavy; masseteric crests prominent; masseteric fossa ending below hypoconid of M_1 with small scar anterior to it below protoconid of M_1; molars as long or longer than wide; anteroconid large; mesostylid distinct, set off from entoconid.

Description. The jaw is very heavy, about as in *Protosciurus condoni,* and more so than in *P. mengi.* The masseteric fossa and crests are correspondingly deep and prominent. M_1 and M_2 are essentially identical in structure, M_2 being somewhat the larger. The large entoconids are set off from the mesostylids by sharp grooves. The anteroconids are better defined and the mesoconids relatively a little smaller than in *P. mengi*. There is no shelf at the base of the mesoconid and the buccal valleys are shallow. The most striking character is the anteroposterior elongation of the molars.

Discussion. In most respects *P. tecuyensis* is similar to *P. condoni* of the John Day. It differs from the latter in the greater length of the molars in relation to their width. At present no descendants of *P. tecuyensis* can be recognized.

Measurements

Depth below anterior end M_1	9.0
Alveolar length P_4-M_3	13.4

PROTOSCIURUS RACHELAE[1] n. sp.

Plate 6

Type. A.M.N.H. No. 7241, a partial left maxilla and premaxilla with I, M^1-M^3.

Hypodigm. Type and U.O.M.N.H. No. F-5039, a fragment of right mandible with M_1-M_3.

Horizon and locality. John Day Formation, probably early Miocene, exact horizon not recorded. John Day Basin, Oregon.

Diagnosis. Smaller than *P. condoni* and *P. tecuyensis;* lophs of M^1-M^2 very low; conules absent; M_1-M_2 wider in relation to length than in *P. condoni, P. mengi,* or *P. tecuyensis;* no mesoconid; posterolophid low.

Description. Only that part of the premaxilla surrounding the anterior end of the incisor and bordering the incisive foramen is preserved. There is no pit in the premaxilla posterior to the incisor for the insertion of a dorsal cheek pouch muscle. The relationship of the infraorbital foramen to the zygomatic plate is clearly demonstrated in that section of the maxilla that is preserved. The infraorbital foramen opens just anterior to and slightly above P^3 and the canal is moderately long as in *P. condoni*. However, the foramen is much more compressed in *P. rachelae* and is a vertical slit. This greater compression is probably due to a

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[1] Named for Rachel H. Nichols whose work at the American Museum on the behalf of paleontologists throughout the world will always be remembered.

somewhat more extensive zygomatic plate lateral to the infraorbital foramen in *P. rachelae.* The masseteric tubercle is large and lies at the ventrolateral corner of the infraorbital foramen. The zygomatic plate is restricted to that part of the maxilla that forms the anterior root of the zygomatic arch lateral to the infraorbital foramen. The plate probably passed above the infraorbital foramen but this portion of the arch is not preserved. The zygomatic plate is concave and faces anterolaterally more so than in *P. condoni* and the plate area appears to be relatively larger in *P. rachelae* than in *P. condoni.* The zygomatic notch is opposite the posterior half of P^4.

P^3 and P^4 are represented only by their roots. M^1-M^3 are low crowned, increase in size from front to back, and have low, rounded, complete lophs. M^1 and M^2 are subquadrate with expanded protocones. There is no indication of either protoconules or metaconules. The anterior cingulum is only moderately expanded and lacks a large, steep parastyle. The incisor is not greatly compressed; it is flattened internally and gently rounded externally. The enamel extends one-third of the way down the external surface but does not overlap onto the internal surface.

Too little of the mandible is preserved to be sure of the extent of the masseteric fossa but it would appear to have terminated below the center of M_1. The molars are quadrate and increase in size from M_1 to M_3. They are moderately worn but all details of the crown pattern are readily discernible. M_1 and M_2 are nearly identical in shape and pattern, with M_2 being slightly larger. They are wider than long and on each the entoconid is distinct and the entoconid corner angular. The trigonid is only slightly higher than the talonid and the trigonid basin is extremely small. The metalophid, although worn, appears to have been complete. The posterolophid is low. A small mesostylid is present. The buccal valley is shallow and shows no trace of a mesoconid. There is little or no development of an anteroconid. M_3 is expanded posteriorly with an enlarged hypoconid and an entoconid that is almost completely submerged in the posterolophid.

Discussion. *P. rachelae* is smaller than *P. condoni* and differs from it in several other respects. The zygomatic plate appears to be somewhat more fully developed in *P. rachelae,* approaching the condition seen in *Miosciurus ballovianus. P. rachelae* also resembles *M. ballovianus* in the absence of conules in the lophs of M^1-M^2. However, the low, rounded lophs and broad protocones of *P. rachelae* tend to ally it with *Protosciurus* rather than *Miosciurus. P. rachelae* resembles *P. mengi* in many details of the lower dentition but differs from it in having much lower trigonids, distinct entoconids, and somewhat lower, more rounded cusps.

There is nothing that would exclude *P. rachelae* from the ancestry of later tree squirrels and several characters seen in the species suggest this. These are: (1) the shape of M^1-M^2 which are wider than long; (2) the low rounded protolophs and metalophs; (3) the absence of conules; (4) the broad protocones; (5) the low trigonids and posterolophids; (6) the distinct entoconids; and (7) the angular entoconid corners of M_1-M_2. *P. rachelae* represents an advance over *P. condoni* toward the tree squirrel condition, and quite probably stands in direct ancestry to later tree squirrels.

Measurements of the cheek teeth of the species of *Protosciurus*

		P. condoni	*P. mengi*	*P. tecuyensis*	*P. rachelae*
P^3	a-p	1.5			
	tr.	1.9			
P^4	a-p	3.2			
	tr.	3.6			
M^1	a-p	3.4			1.9
	tr.	3.8			2.4
M^2	a-p	3.6, 3.6			2.0
	tr.	4.0, 4.0			2.6
M^3	a-p	4.2, 4.2			2.3
	tr.	4.0, 4.0			2.3
P_4	a-p	3.2	2.5		
	tr.		2.2-2.5		
M_1	a-p	3.3	2.5	3.1	2.2
	tr.	3.4-3.4	2.7-2.8	2.8-3.1	2.3-2.5
M_2	a-p	3.6	2.8	3.4	2.4
	tr.	3.8-3.8	3.0-3.1	3.1-3.2	2.7-2.7
M_3	a-p	4.4	3.2		2.6
	tr.	3.8-3.4	3.0-2.6		2.5-2.1

Sciurus sp.

Sciurus sp. Wallace, 1946, p. 123.

Referred material. L.A.C.M. (C.I.T.) Nos. 3076 and 3078, both specimens are right maxillary fragments with M^2-M^3. In L.A.C.M. (C.I.T.) No. 3076 the right M^2-M^3 are preserved along with the alveoli of P^3-M^1, a portion of the palate, part of the zygomatic plate, and the masseteric tubercle and infraorbital foramen.

Horizon and locality. Hemingfordian, Middle Miocene, Beatty

Butte Tuffs exposed on E. side of Beatty Butte, 24 miles SW. of Blitzen, Oregon.

Description. The infraorbital foramen is lateral to and only slightly above the masseteric tubercle. It is compressed but the long axis is more nearly horizontal than vertical. The masseteric tubercle is low and situated just anterior to the alveolus for P^3. The zygomatic plate does not appear to be as fully developed as in Recent sciurids, judging from the inclination of the infraorbital foramen. It faces downward and forward and does not rise as steeply towards the superior surface of the rostrum as it does in Recent forms. This incomplete development is also reflected in the more horizontal position of the infraorbital foramen which has not yet been compressed into a vertical slit by the upward expansion of the masseter.

The second upper molar is quadrate in outline with a broad protocone and low lophs without conules. The anterior cingulum is relatively narrow and the parastyle low. There is a very large mesostyle on the buccal margin of the tooth. M^3 is triangular with a broad protocone and expanded posterior cingulum which passes diagonally from the protocone to the postero-buccal corner of the tooth. The paracone is high and the protoloph drops abruptly away from it to the protocone. The anterior cingulum and parastyle are small.

Discussion. These specimens clearly indicate the presence of *Sciurus* in this late Hemingfordian fauna but the material is much too fragmentary to indicate any precise relationship to modern species. It does, however, appear to be fully as advanced as the Recent forms, and, in the dentition, resembles *S. carolinensis* more than any other species.

GENUS AND SPECIES INDETERMINATE

Plate 7, figure 1

Referred specimen. Y.P.M. No. 13602, a right mandible with I, P_4-M_3, lacking the ascending ramus and angle.

Horizon and locality. Arikareean, early Miocene. John Day Valley, Oregon.

Description. The mandible is slender and shallow with a long diastema and shallow diastemal depression. The mental foramen lies somewhat below the diastemal level midway between P_4 and the anterior extremity. The masseteric fossa extends forward under the posterior half of P_4 and is sharply pointed anteriorly. That part of the area of insertion of *M. temporalis* behind M_3 is a well defined pit with an elevated ridge along the medial side.

P_4 is trapezoidal with closely appressed protoconid and metaconid. These cusps are separated by a narrow but deep notch. The ectolophid is low and bears a large mesoconid, which fills the shallow buccal valley. The posterolophid is curved and the entoconid submerged within it. There is a notch between the end of the posterolophid and the metaconid and no indication of a mesostylid. M_1 and M_2 are compressed anteroposteriorly and relatively wide. The trigonid basins are very small and completely enclosed. There is no indication of an anteroconid on either tooth. The ectolophids are low and the buccal valleys shallow. The posterolophids are low and pass almost directly transversely across the teeth to end in distinct entoconids. There is a deep notch between the entoconids and the prominent mesostylids. M_3 is triangular with a moderately expanded hypoconid and a posterolophid that is slightly constricted at the entoconid. There is a distinct notch between the entoconid and the small mesostylid.

Discussion. This specimen has an extremely advanced masseteric structure which is quite in contrast to that seen in the other John Day sciurids. The dentition is closer to that of *Protosciurus* and *Sciurus* than to that of other squirrels. M_1-M_2 are, however, somewhat wider in relation to their length than they are in *Protosciurus* and *Sciurus* and the notch between the entoconid and mesostylid is more prominent than in either of those genera. In this respect the specimen is somewhat reminiscent of *Glaucomys*.

Measurements

Depth at mental foramen		5.22
Depth below M_1		6.53
Alveolar length P_4-M_3		8.22
Occlusal length P_4-M_3		8.02
	a-p	tr.
P_4	1.75	1.50-1.85
M_1	1.85	2.20-2.35
M_2	2.00	2.50-2.50
M_3	2.30	2.40-2.05

TRIBE MARMOTINI Simpson 1945

Limbs relatively short, stout; distal ends of radius and ulna, and tibia and fibula broad; three to four sacral vertebrae; skull roof flat to moderately convex; zygomatic plate inclined at 50°

or less in relation to basicranial axis; skull relatively narrow interorbitally; diastema long, diastemal depression shallow; anterior end of mandible at or above level of alveolar border; upper molars triangular to subquadrate; metaconules usually well developed; entoconids indistinct and incorporated in posterolophids (except in *Arctomyoides* and *Protospermophilus*); lingual portion of lower molars generally more greatly compressed anteroposteriorly than buccal portion.

Range. Early Miocene to Recent in North America.

PALAEARCTOMYS Douglass

Type species. Palaearctomys montanus Douglass.

Diagnosis. Rostrum broad, deeper than in *Marmota*; zygomatic plate failing to reach dorsal surface of rostrum; infraorbital foramen slit-like; masseteric tubercle small, set well below infraorbital foramen; zygomatic arch slender; palate broad; postpalatal vacuities present just above internal nares; postorbital processes large, with no posterior curvature; diastemal region of mandible extremely heavy; molars small in relation to size of skull; upper incisors grooved, lower incisors with many fine longitudinal striations.

Range. Probably late Miocene (Barstovian).

PALAEARCTOMYS MONTANUS Douglass

Plates 8, 9

Palaearctomys montanus Douglass, 1903, p. 183.
Palaearctomys macrorhinus Douglass, 1903, p. 184.

Type. C.M. No. 740, poorly preserved skull without dentition, basicranium, most of occiput, nearly complete right and left mandibles, and a few skeletal elements.

Type of synonym. C.M. No. 733, well preserved skull lacking the nasals, left zygomatic arch, occipital region and basicranium, and RP^4, M^{2-3}, LM^{1-3}

Hypodigm. The types only.

Horizon and locality. Lower Madison Valley Formation, probably Barstovian, late Miocene. Gallatin County, Montana.

Diagnosis. As for the genus.

Douglass (1903) described two species of *Palaearctomys*, both based on skulls from the Lower Madison Valley. One specimen, C.M. No. 733, was in excellent condition while the other, C.M. No. 740, was badly broken. The latter was made the type of *P.*

montanus. This skull was reconstructed using an excessive amount of plaster and a Recent marmot skull as a model. The reconstruction thus resembled the Recent *Marmota monax* in most respects. This condition was quite in contrast to that displayed in the uncrushed skull. Consequently, the well preserved skull was made the type of *P. macrorhinus* and from the description of each species (Douglass, 1903, pp. 182–186) little comparison was made between the two. Bryant (1945) discussed both species but again made no real comparison of the two except as noted in his diagnosis.

It is quite obvious that these two skulls belong to the same species, once due allowance has been made for the plaster in the type skull. Measurements of all areas where the original bone has not been distorted, such as length of palate and depth of rostrum, are nearly identical for the two skulls. Also, the postpalatine vacuities occur in both specimens and are unknown in any other sciurid. The material is therefore considered to represent one species, *Palaearctomys montanus*.

Description. The skull is heavy and although of approximately the size of that of *Marmota monax* is considerably deeper through the rostrum and orbital region. As in *Marmota*, the skull roof is flat, the postorbital processes large, and the skull narrow behind the postorbital processes. The sagittal crest is prominent, especially in C.M. No. 740 where the temporal ridges are fused opposite the squamosal root of the zygomatic arch. The zygomatic arch is expanded posteriorly, although not to the extent seen in *Marmota*, and the jugal is somewhat twisted so that it does not lie in the vertical plane, although not as much so as in the ground squirrels. The arch is extremely thin and there is no well defined fossa marking the origin of the posterior part of the *M. masseter lateralis* as there is in *Marmota*. The nasofrontal sutures, and the premaxillary-frontal sutures form a straight line across the roof of the skull parallel to the anterior edge of the orbit. This is quite in contrast to the condition in *Marmota* where the nasals extend posteriorly well beyond the premaxillary-frontal sutures. The extent of premaxillary-frontal contact is also greater in *Palaearctomys* than in *Marmota*. The nasals expand as they pass anteriorly; they do not extend anteriorly in advance of the incisors. The premaxillary-maxillary suture passes anteriorly to the dorsal lip of the zygomatic plate and then descends in a straight line down the rostrum and across the palate to the incisive foramen. The *M. masseter lateralis* appears to have been limited to the maxilla. The zygomatic plate does not reach the dorsal surface of the rostrum but terminates at the level of the incisor alveolus. There is a slight depression in the maxilla just below its dorsal extension. The lateral edges of the anterior zygomatic roots do not overhang the plate area as they do in *Marmota.* The infraorbital foramen is a vertical slit set rather high on the side of the rostrum; the canal is short. The zygomatic notch is opposite the contact between P^4-M^1. The masseteric tubercle is extremely small, lying just anterior to P^3 and well below the infraorbital foramen; a low, rugose ridge runs from it to the base of the infraorbital foramen. The palate is broad and the tooth rows nearly parallel. The palatine-maxillary suture extends forward to the level of the middle of M^1, where, in contrast to the condition in *Marmota,* it is transverse. Beginning opposite M^3 and extending back below the internal nares there are two large postpalatal fossae that appear to lie completely within the palatines. These fossae resemble those occurring in geomyids; however, they do not appear to have foramina at their anterior ends, as do those of *Geomys.* Near the posterior border of the lateral wall of each fossa there is a rather large opening. These openings may be due to breakage but they could also be foramina. What function the fossae may have served is unknown; comparable structures are not known in any other sciurid, fossil or Recent. The internal nares open much farther posteriorly than in *Marmota,* due to the presence of these fossae. The buccinator and masticatory foramina are fused. The paroccipital processes are stout and stand well away from the bullae.

The mandibles are extremely heavy and deep, much more so than in *Marmota* or in *Arctomyoides.* The diastemal area in particular is short, very deep and greatly swollen lateral to and above the incisor. The anterior tip of the mandible lies about on the level of the alveolar border. The dorsal surface of the mandible drops steeply anterior to P_4 and then curves upward to the rim of the incisor alveolus. The mental foramen lies about two-thirds of the way up the side of the mandible and midway between the incisor and P_4. The ventral masseteric crest is strong. The ascending ramus rises opposite the anterior end of M_3; its anterior border forms a continuous slope. The condyle is broad and lower than in *Marmota.*

Judging from the size of the alveolus, P^3 was rather small, as are all of the cheek teeth in relation to skull size. P^4 is incomplete, lacking the anterior cingulum and much of the protoloph. The protocone appears to have been broad. The posterior cingulum is small, the metaloph low and complete, with the metaconule completely subordinated within it. A large mesostyle is present. M^1-M^2 are subquadrate in outline with expanded protocones. The protolophs and metalophs are low, complete, and there is no metaconule. The anterior cingula are only moderately expanded and the parastyles are small, both notable differences from *Marmota.* The mesostyles are large. M^3 is triangular in outline with only a slight expansion of the posterobuccal portion of the tooth. The upper incisor is extremely heavy and almost triangular in outline. There is one well marked groove on the anterior face as well as innumerable fine longitudinal striations.

The known lower cheek teeth are all so worn that some of the pattern has been obliterated. P_4 is smaller than M_1 and is trapezoidal in outline. The protoconid and metaconid are set close together but there is a distinct deep notch between them; anteriorly, they are united by a small anteroconid. The ectolophid is low and bears a mesoconid. The posterolophid is low and terminates in a distinct entoconid. A narrow notch separates the entoconid from the large mesostylid. M_1-M_2 are rectangular in outline. They are wider than long and the buccal and lingual widths are equal. There is no trace of an anteroconid, a mesoconid, or a mesostylid on any of the molars. The metalophid was evidently incomplete on all and the trigonid not greatly elevated above the talonid. The posterolophid on M_1-M_2 is low and passes slightly diagonally from the hypoconid to the distinct entoconid. The buccal valleys are broad and shallow. M_3 is triangular in outline with greatly enlarged hypoconid and posterolophid. The lower incisors are very compressed and flattened both medially and laterally. They are much larger than in Recent species of *Marmota.* They are not distinctly grooved as are the upper incisors but the enamel bears many fine longitudinal striations.

Discussion. Palaearctomys resembles *Marmota* in a general way and is certainly closer phylogenetically to it than to other sciurids. Nevertheless, it differs in a great many characters, the most striking of which are the small size of the cheek teeth and large size of the incisors in relation to skull size. The presence of postpalatal fossae is also unique in this genus. This would indicate a rather early separation of the *Palaearctomys* line. There appears to be no close relationship between *Palaearctomys* and *Arctomyoides* or *Paenemarmota.* These three genera probably represent as many offshoots within the Marmotini, none of which has left any descendants.

Measurements

	C.M. No. 740	No. 733
Depth of rostrum (taken just anterior to dorsal termination of zygomatic plate)	24.0	23.9
Width of rostrum	21.2	22.2
Length of palate (posterior edge of incisors to internal narial opening)	46.4 (approx.)	44.7
Interorbital width (behind postorbital processes)	20.8	20.0
Length mandible (anterior tip of incisor to condyle)	70.5	—
Length of diastema	16.8	—
Depth of mandible at mental foramen	12.7	—
Depth of mandible under M_1	17.7	—
Alveolar length P^3-M^3	—	15.4
Alveolar length P_4-M_3	15.1	—

C.M. No. 733				C.M. No. 740	
	a-p	tr.		a-p	tr.
RP^4	3.30	3.60	RI_1	7.20	3.30
RM^2	3.80	4.30	RP_4	3.30	3.00-3.30
RM^3	4.30	4.10	RM_1	3.40	3.80-3.80
LM^1	3.50	4.10	RM_2	3.60	4.30-4.20
LM^2	3.80	4.30	LI_1	7.20	3.30
LM^3	4.20	4.10	LP_4	3.40	3.00-3.30
			LM_1	3.30	3.80-3.80
			LM_2	3.60	4.30- —
			LM_3	4.20	4.20-3.70

ARCTOMYOIDES Bryant

Type species. Sciurus arctomyoides Douglass.

Diagnosis. Diastemal depression shallow and long, dropping gently from P_4; superior border of masseteric fossa nearly reaching alveolar border; upper incisor with distinct median longitudinal groove; lophs on M^1 complete, low; protocone, anterior cingulum broad; M^1 subquadrate; M_1-M_2 nearly square in outline, entoconids large, ectolophids weak, metalophids incomplete.

Range. Late Miocene (Barstovian).

ARCTOMYOIDES ARCTOMYOIDES (Douglass)

Plate 7, figure 2

Sciurus arctomyoides Douglass, 1903, p. 181.
Arctomyoides arctomyoides Bryant, 1945, p. 361.

Type. C.M. No. 741 incomplete premaxillae and partial right maxilla with right and left I^1 dP^3-dP^4 and M^1, RI_1, nearly complete left mandible with dP_4-M_3, incomplete I_1.

Hypodigm. Type only.

Horizon and locality. Late Miocene, Lower Madison Valley Formation near Logan, Gallatin County, Montana.

Diagnosis. As for genus.

Description. The upper incisors are not greatly compressed and their anterior faces bear many fine longitudinal striations and a single median groove. The deciduous third premolar is a very small peg-like tooth that fits against the anterointernal portion of dP^4. The anterior cingulum and parastyle of dP^4 are large, making the tooth much longer buccally than lingually. The protocone occupies most of the lingual border. The protoloph is low, complete, without conules, and passes directly across the tooth. The metaloph is low and passes anteromedially to the protocone; it is only partially constricted at the protocone and lacks a distinct metaconule. The mesostyle is well developed and the posterior cingulum small. M^1 is nearly quadrangular in outline. The protocone is very broad and there is a small cuspule at the junction between protocone and posterior cingulum. The lophs are low and without conules. The anterior cingulum is broad and the parastyle high but not as well developed as on dP^4. The mesostyle is large.

The horizontal ramus of the mandible is massively built beneath the cheek teeth, more slenderly in the symphysial region. The diastemal portion of the mandible is long and shallow, sloping gently away from dP_4. The mental foramen lies near the center of the lateral surface of the symphysial region beneath the midpoint of the diastema. The masseteric fossa is deep and lies high on the side of the mandible with its superior border almost merging with the alveolar border. It is gently rounded anteriorly, terminating below the anterior end of M_1. Bryant (1945, p. 362) states that the dorsal surface of the condylar process is in the same plane as the alveolar border, but this is not the case. The ascending ramus has been crushed and forced somewhat downward and the condyle itself is missing; with proper restoration the process would actually be well above the alveolar border. The anterior border of the coronoid process merges with the alveolar border opposite the protoconid of M_2.

The lower incisors are greatly compressed and have many fine longitudinal striations on their anterior faces; the incisors taper considerably toward their tips, due to the extreme youth of the specimen. dP_4 is much longer than wide and is considerably smaller than M_1. The protoconid and metaconid are widely separated and joined anteriorly by a heavy, short, anterior cingulum. The metalophid is weak but does close off the trigonid basin posteriorly. The posterolophid curves gently from the hypoconid to the distinct entoconid. The ectolophid is partially elevated and set close to the buccal margin. Neither mesostylid nor mesoconid is distinct. M_1 and M_2 are essentially identical in structure, except that the anterior cingulum joins the protoconid at a somewhat greater angle on M_1, the trigonid basin being thus slightly more rounded on M_1. On both teeth the metalophid is weak; the protoconid and hypoconid are of equal size and are joined by an elevated ectolophid bearing a prominent mesoconid; the posterolophid is curved, ending in a large entoconid; a large mesostylid is present. M_3 is not much larger than M_2 but differs from that tooth in having a greatly expanded hypoconid and a crenulated posterolophid that curves much more sharply from the hypoconid to the metaconid; entoconid and mesostylid are lost to view among the crenulations.

Discussion. Douglass assigned this species to *Sciurus,* stating (1903, p. 182) "the teeth are intermediate between those of *Sciurus* and *Arctomys,* rather more resembling some species of the former." Bryant placed the species in a new genus, *Arctomyoides,* observing that it was closer to *Marmota* than to *Sciurus* (he mistook dP^4 for P^4 but recognized the presence of dP_4) in many characters of the dentition. These included (1945, p. 362) "enlarged parastyles, protocones of P^4-M^1 small and teeth consequently triangular in occlusal outline, protolophs and metalophs convergent toward the protocones rather than parallel, ectolophids elevated and situated well in from the margins of the molars, talonid basins deep and longer than wide, posterolophids crescentic, diastemal portion of mandibular ramus long and shallow and its anterodorsal border as high as the alveolar border, and the dorsal surface of the condyloid process is level with the mandibular tooth row." Certain of these characters do not indicate as close a relationship to *Marmota* as Bryant believed. The parastyle on M^1 is enlarged but no more so than in the protospermophiles and not as much so as in *Marmota.* It is high on dP^4 but it is generally much higher on dP^4 than on P^4 in all groups of sciurids. The protocone on M^1 is actually nearly as wide as the lingual margin of the tooth making the tooth subquadrate rather than triangular. The protolophs and metalophs are no more convergent than in *Sciurus niger* or *S. carolinensis.* The ectolophids are more elevated and set further in than in *Sciurus* but they do not approach the condition seen in *Marmota vetus, Marmota minor,* or Recent marmots. The talonid basins are more as in *Marmota* as regards depth, but in *Marmota* they are wider than long, just the reverse of what is seen in *Arctomyoides.* The posterolophids are somewhat curved, more so than in *Sciurus* but less so than in *Marmota.* The mandible differs from both *Sciurus* and *Marmota* in its construction. Other differences between *Arctomyoides* and *Marmota* were noted by Bryant and include the presence of large mesoconids and entoconids.

It seems evident that *Arctomyoides* possesses a suite of characters that sets it apart from both *Sciurus* and *Marmota.* In fact it is just as close to *Protospermophilus* as to either of them, particularly in the structure of dP^4-M^1. On the evidence, I believe that *Arctomyoides* was probably an early offshoot from the line leading to *Marmota* from *Protospermophilus. Arctomyoides* evolved certain specializations of its own, such as the increased length of the molars, the high position of the masseteric fossa on the side of the jaw, and a long, shallow diastema, and independently acquired such marmot specializations as the increased prominence of the ectolophid.

Measurements

Diastemal length	13.0
Depth below P$_4$	11.0
Depth below M$_1$	11.8
Alveolar length dP$_4$-M$_3$	15.5

	a-p	tr.		a-p	tr.
dP^3	1.20	1.20	dP$_4$	3.30	2.50-3.10
dP^4	3.40	3.20	M$_1$	4.00	4.00-4.10
M^1	3.90	4.40	M$_2$	4.20	4.40-4.40
I	2.30	3.80	M$_3$	4.30	4.40-3.80
			I	4.00	2.00

PAENEMARMOTA Hibbard and Schultz

Type species. Paenemarmota barbouri Hibbard and Schultz

Emended diagnosis. "A ground squirrel (Tribe Marmotini) belonging in the "Terrestrial Squirrel Section" of Bryant (1945, p. 372); larger than all other known ground squirrels. Lower teeth with base of incisor well behind M_3, rather than beneath (incisor crosses beneath M_{2-3} and its base forms a slight swelling on the external surface of the ascending ramus slightly beneath alveolar plane); P_4 larger than M_1 and progressively molariform; all four cheek teeth with rugose talonid basins and basin trench along ectolophid and metalophid margins of basin and individually varying in extent along posterolophid margin of basin; protoconid larger than in *Marmota* and about as high as parametaconid in unworn teeth; mesoconid present or absent on the ectolophid of M_3 and P_4, and lower incisor with longitudinal striations. Upper teeth with P^4 as large as, or larger than M_1; metaconule well developed on P^4 and absent or only slightly developed on molars; posterior cingulum prominent across width of tooth because of broad posterior valley; M^3 with well-developed metaloph that is more or less parallel to protoloph and separated from protocone in unworn teeth; M^3 also with broad posterior valley with or without a rugose floor but lacking the pronounced posterior lobe of some modern ground squirrels; P^3 with anterior cingulum and double-cusped "protoloph" followed by a distinct valley and loph-like posterior cingulum; upper incisor striated. Masseteric tubercle very prominent; palate more concave (upward) than in *Marmota* and most ground squirrels; cheek pouch rudimentary; lower jaw massive; and masseteric fossa variable in form but without pronounced dorsal crest of *Marmota*." (Repenning, 1962, p. 543.)

Range. Hemphillian of Mexico and early Pleistocene of Nebraska, Kansas, Texas and Arizona.

PAENEMARMOTA BARBOURI Hibbard and Schultz

Type. K.U. No. 6994, a nearly complete left ramus with incisor, P_4-M_3.

Horizon and locality. Early Pleistocene, Rexroad Formation. S.34, T.34S., R.30W., Meade County, Kansas, Locality No. 22.

Diagnosis. As for genus.

Discussion. This genus has recently been reviewed by Charles

A. Repenning (1962) and has not been examined by me. From the published descriptions and illustrations (Hibbard and Schultz, 1948; Repenning, 1962), *Paenemarmota* would appear to be a highly specialized offshoot of the true *Marmota* stock. The genus appears to have little in common with *Palaearctomys* or *Arctomyoides*. It does resemble *Marmota nevadensis* in certain respects, however, particularly in the rugose talonid basins and overall size and shape of the dentition. P_4 of *M. nevadensis* is not as large as that of *Paenemarmota*, however.

Repenning believes *Paenemarmota* to be possibly more closely related to *Citellus* than to *Marmota* although he states that sufficient fossil evidence is not available at present to be certain of exact relationships. From his descriptions and illustrations, *Paenemarmota* would appear to me to have been derived from the *Marmota* lineage probably just shortly after the marmots arose from the protospermophiles. The enlarged P^4_4, the presence of mesoconids in the Pliocene material, the general shape of the teeth, and the absence of mesostylids with the resulting rather broad gap between the entoconid and metaconid all tend to ally *Paenemarmota* with *Marmota*. The differences in the heaviness of the dorsal border of the masseteric fossa and the presence of the basin trench of the talonid would not contradict this relationship. Both dorsal and ventral masseteric crests vary widely in prominence in samples of *Marmota monax* and, while the dorsal crest is not prominent in *Paenemarmota*, I would not consider this character of equal weight in determining relationships with some dental and other mandibular characters. The presence of the basin trench is dependent upon the development of ridges or cuspules in the talonid basin and can be found in both the spermophile and marmot groups. On the evidence available, I would favor a closer relationship to *Marmota* than to *Citellus* for *Paenemarmota*.

MARMOTA Frisch

Type species. Mus marmota Linnaeus.

The genus *Marmota* is very poorly represented in the fossil record with only three pre-Pleistocene records known at present. Marmots first appear in the early Pliocene of Nebraska and can be traced through the Pliocene. However, the lineages of modern species cannot be traced back into the Pliocene with any degree of accuracy. *M. vetus* of the Clarendonian and *M. minor* of the Hemphillian are both much smaller than the Recent species but show the enlargement of P_4, the narrow lingual borders of M_1-M_2.

and the reduced M_3^3 characteristic of all modern forms. *M. nevadensis* from the Hemphillian is not closely related to either *M. vetus* or *M. minor* and certainly was not ancestral to Recent species of the genus. Nevertheless, it is even further removed from *Palaearctomys* and *Arctomyoides* and is therefore retained in *Marmota* for the present.

Range. Early Pliocene to Recent in North America.

MARMOTA NEVADENSIS (Kellogg)

Plate 10

Arctomys nevadensis Kellogg, 1910, p. 422.

Marmota nevadensis Wilson, 1937b, p. 34; Bryant, 1945, p. 363.

Type. U.C.M.P. No. 12506, the anterior portion of a left mandible with broken incisor, P_4-M_1.

Hypodigm. Type of U.C.M.P. No. 12544, RI_1, RP_4, and half of LP_4.

Horizon and locality. Hemphillian, late Pliocene. Locality 1105 near Thousand Creek, Humboldt County, Nevada.

Emended diagnosis. Ramus larger and more massive than in any other species of *Marmota;* P_4 not molariform, as long as but narrower than M_1; talonid basins of P_4-M_1 with complex cuspules and/or low ridges.

Description. The jaw is extremely robust and especially heavy below M_1. In contrast to *Palaearctomys,* the anterior portion of the diastemal area is not swollen, and the diastemal depression is shallow anterior to P_4. The mental foramen lies just anterior to P_4 and about two-thirds of the way down the ramus. The poorly marked anterior termination of the masseteric fossa lies below the anterior end of M_1.

The incisor is not as strongly recurved as that of *Palaearctomys,* is moderately compressed and bears many prominent longitudinal grooves. P_4 is about as long as M_1 but neither as wide nor as molariform. The protoconid and metaconid are closely appressed and there is a strong anterior cingulum between these cusps about halfway down the anterior face of the tooth; an anteroconid is lacking. The trigonid basin is small and the trigonid is elevated well above the talonid basin. The ectolophid is a high crest set far in from the buccal margin. A small mesostylid at the base of the metaconid is partially set off from the posterolophid by a shallow notch. The posterolophid curves in a smooth arc through the entoconid which is completely submerged within it. The posterolophid is crenulated and steeply elevated above the deep talonid basin. Within the basin are six cuspules arranged in pairs and running postero-buccally from the mesostylid. M_1 is rhomboidal in outline. The trigonid pit is completely enclosed and set high above the talonid basin. As on P_4, the strong anterior cingulum bears no anteroconid. The ectolophid and posterolophid are high. Three ridges running from the lingual border into and fusing within the talonid basin correspond serially to the cuspules on P_4. The mesostylid is small but distinct, and set off from the posterolophid by a shallow depression.

Discussion. Bryant (1945, p. 363) considered *Marmota nevadensis* to be intermediate between *Arctomyoides* and the Recent *Marmota.* This appears to me not to be the case. *M. nevadensis* differs markedly from Recent species of *Marmota* in such characters as its much more massive mandible and the accessory talonid cuspules. *M. nevadensis,* nevertheless, does appear to be closer to the true marmot line of descent than do either *Arctomyoides* or *Palaearctomys,* although certainly not ancestral to any Recent species of *Marmota. M. nevadensis,* while showing some resemblance to *Paenemarmota,* especially in the possession of ridges and tubercles in the talonid basins of P_4-M_1 (a point of resemblance to *Cynomys* also), nevertheless, differs quite markedly in having much more strongly developed trigonid lophids with enclosed trigonid pits, and in the smaller size of P_4 in relation to M_1. Finally, *M. nevadensis* is quite different from *M. vetus* and from the descendant species, *M. minor* (also from the Thousand Creek fauna), a form which certainly does appear to be on the main evolutionary line leading to Recent *Marmota. M. nevadensis* probably diverged from the main line of marmot development sometime in the late Miocene or early Pliocene.

Measurements

Length of diastema	20.6
Depth of mandible below mental foramen	approx. 14.5
Depth of mandible below P_4	approx. 20.0

Type		a-p	tr.
U.C.M.P. No. 12506	LP_4	7.00	5.00-6.30
" "	LM_1	6.40	6.60-7.00
U.C.M.P. No. 12544	RI_1	6.80	4.50
" "	RP_4	6.90	5.60-6.80

MARMOTA VETUS (Marsh)

Plate 11, figure 1

Arctomys vetus Marsh, 1871, p. 121.
Palaearctomys vetus Matthew, 1909, p. 116; Bryant, 1945, p. 360.

Type. Y.P.M. No. 10323, a left ramus lacking the angle and anterior portion of the diastema.

Hypodigm. Type only.

Horizon and locality. Miocene or Pliocene, "Loup Fork Beds" northern Nebraska; "in the Pliocene beds, on the Loup Fork in northern Nebraska" (Marsh, 1871, p. 121).

Diagnosis. Smallest known species of *Marmota*; ectolophids strong on P_4-M_3; M_1-M_2 compressed anteroposteriorly; P_4 elongate; metalophid complete on M_1, not on M_2-M_3; single median groove on lower incisor.

Description. The dorsal surface of the mandible drops steeply anterior to P_4 and the diastemal depression is deep. The mental foramen lies just anterior to P_4 and approximately one-third of the way down the side of the diastema. The masseteric fossa ends bluntly below the anterior end of M_1. It is deeply concave with a strong inferior and a weak superior ridge. The alveolus of the incisor terminates just below the coronoid process in a distinct rounded knob. The condylar process is long and inclined more backward than upward.

P_4 is nearly as long as M_1. However, it is not molariform and is much narrower than the molars. The protoconid and metaconid are rather closely appressed with only a shallow valley separating them anteriorly. A prominent ridge passes down the anterior face of the protoconid but does not join the metaconid. The posterolophid is elevated and the entoconid is completely incorporated within it. Lingually, there is a distinct notch between the metaconid and posterolophid with no indication of a mesostylid. The ectolophid is high and thick on all the cheek teeth but there is no sign of a mesoconid on any of them. M_1-M_2 are compressed anteroposteriorly, with M_1 being somewhat smaller. The talonid basin is quite deep on both and is rimmed by high ectolophids and posterolophids. The metalophid is complete on M_1 but not on M_2. Small mesostylids are barely distinguishable on the slopes of the metaconids, which are themselves separated by slight notches from the posterolophids. On M_3, the metalophid is still weaker than on M_2 and passes into the talonid basin. The posterior half of M_3 is expanded considerably with a greatly enlarged hypoconid and a heavy, steep posterolophid that passes almost without interruption into the metaconid slope.

Discussion. *Marmota vetus* is obviously closely related to the true marmots. Matthew placed it in *Palaearctomys* and Bryant followed suit. Neither author examined the type specimen. *M. vetus* differs from *Palaearctomys* in the larger size of P_4-M_3 relative to overall size, the greater anteroposterior compression of M_1-M_2, and the complete submergence of the entoconid within the posterolophid. *M. vetus* resembles *Marmota monax* and *M. flaviventris* in nearly all respects except size, a character which offers no drawbacks in evolving the Recent marmots from *M. vetus* through *M. minor.*

M. vetus resembles *Protospermophilus oregonensis* in some respects and it may have evolved from the protospermophile ground squirrels. The diastema is longer in *P. oregonensis* but the mandible resembles that of *M. vetus* in all other characters. There are several differences in the dentition between these species, particularly the presence of large entoconids and mesoconids in *P. oregonensis*. However, the general shape of the lower cheek teeth is similar in the two forms and the lingual compression of M_1-M_2 is also suggestive of possible relationship. Most of the early spermophiles while having rounded posterointernal corners on M_1-M_2 lack this lingual compression of the teeth. However, enough is not known at present about the spermophiles and early marmots to rule out a spermophile ancestry for *Marmota.*

Measurements

Length of mandible	approx. 38.0
Length of diastema	approx. 6.8
Depth of mandible below mental foramen	approx. 6.2
Depth of mandible below M_1	9.2
Alveolar length P_4-M_3	14.0

MARMOTA MINOR (Kellogg)
Plate 11, figure 2

Arctomys minor Kellogg, 1910, p. 425.
Marmota minor Wilson, 1937b, p. 34; Bryant, 1945, p. 363.

Type. U.C.M.P. No. 12538, maxillary and mandibular fragments with LP^3-P^4, RM^2-M^3, LM_2-M_3, RP_4, RM_1-M_2, upper and lower incisors, and various skeletal fragments.

Hypodigm. Type only.

Horizon and locality. Hemphillian, middle Pliocene. Locality No. 1083 at Thousand Creek, Humboldt County, Nevada.

Emended diagnosis. Larger than *Marmota vetus,* smaller than Recent species; cheek teeth mesodont; P^3 relatively large; metaconules prominent; metalophs slightly constricted; P_4 longer than M_1-M_2, almost as wide; metalophids on M_1-M_3 less reduced than in Recent species, more reduced than in *M. vetus;* posterolophids relatively low.

Description. The mandible, so far as revealed by the fragments preserved, appears to have been of almost the same proportions as that of *Marmota monax.* It is not swollen through the masseteric fossa nor in the diastemal region. The diastemal depression does not drop as abruptly anterior to P_4 as in the Recent species.

P^3 is relatively large, circular in outline, with a high central crest and expanded anterior and posterior shelf areas that are ringed by sharp cingula. P^4 is triangular in outline. The anterior cingulum is expanded and there is a large tricuspate parastylar area. The protocone is a high, pointed cusp; the anterior cingulum joins it near the base while the small posterior cingulum rises almost to the apex. The high and steep protoloph and metaloph pass directly across the tooth to the protocone. The metaconule is large and distinct, and the metaloph is constricted at the protocone. A small mesostyle is present. M^2 is essentially identical in structure except that the anterior cingulum and parastyle are not as expanded. The anterior portion of M^3 resembles that of M^2, being moderately large and the protoloph high and steep. Posteriorly, the buccal half of the posterior cingulum is expanded. From the low metaconule, crests pass to the protocone and to the posterior cingular expansion, and there is a large mesostyle with a short crest passing internally from it.

P_4 is elongate and trapezoidal in outline. The trigonid is narrower and somewhat more elevated than the talonid. There is a strong anterior cingulum well down on the anterior face of the tooth. This encloses a deep trigonid pit bounded posteriorly by the strong metalophid. There is no anteroconid, mesostylid, or mesoconid. The posterolophid is a high and sharp crest, terminating abruptly at the entoconid corner and constricted at its union with the hypoconid. The trigonid basin is open lingually between the entoconid corner and the metaconid but is closed buccally by a low ectolophid. M_1 and M_2 are essentially identical, differing only in the slightly greater development of the metalophid on M_1, which joins the metaconid well down on its slope, isolating a small trigonid pit. On M_2 the metalophid passes into the talonid basin leaving the trigonid basin open posteriorly. M_1-M_2 are compressed anteroposteriorly with rounded entoconid corners and no distinct entoconid. The posterolophids are high and sharp passing through the entoconid area to the lingual margins. They fail to join the metaconids, thus leaving the talonid basin open on the lingual margin. The buccal valleys are wide and closed internally by low ectolophids. M_3, with the exception of its somewhat expanded hypoconid-posterolophid area, is identical with M_1-M_2.

The upper incisors are shallowly grooved and well rounded laterally. The ungrooved lower incisors are very finely striated.

The right and left humeri are represented by the distal segments below the deltoid crests. They agree in most respects with those of *M. monax* but the ectepicondylar process does not appear to have been as expanded as in *M. monax*. A partial right ulna is present which does not differ from that of *M. monax*. The partial right and left radii of *M. minor* are also extremely similar to those of *M. monax* but differ from those of the Recent species in being relatively broader through the distal third of the shaft. A partial left tibia in the collection does not appear to differ from that of *M. monax*. The calcaneum, metatarsals, and phalanges are similar to those of *M. monax*.

Discussion. Marmota minor is structurally intermediate between *M. vetus* and the Recent species. The proportions of M_1-M_2 in *M. minor* have changed from those of *M. vetus* with the length of M_1 equalling that of M_2 in the later species and with M_1 and M_2 becoming wider in relation to their length in *M. minor*. As regards the lower dentition of *M. minor*, it is more advanced than in *M. vetus*, less so than in the Recent forms in the following characters: (1) P_4 longer than M_1-M_2; (2) metalophid of M_1-M_3 reduced; (3) posterior portion of M_3 reduced; (4) diastemal depression deep anterior to P_4. What is known of the skeleton is scarcely distinguishable from that of *M. monax*, but not enough postcranial material is yet known for the species to determine the extent of fossorial adaptation at this stage in marmot evolution. Subsequent marmot evolution involved a general increase in size, an enlargement of P_4, reduction of the posterior portion of M_3, a further anteroposterior compression of M_1-M_2, and probably further fossorial specialization.

Measurements of the cheek teeth
of *Marmota vetus, M. minor,* and *M. monax.*[1]

		M. vetus	*M. minor*		*M. monax*
P^3	a-p		3.0		2.8
	tr.		3.0		3.1
P^4	a-p		4.2		4.6
	tr.		4.4		4.9
M^1	a-p				4.6
	tr.				5.2
M^2	a-p		3.8		4.7
	tr.		4.5		5.6
M^3	a-p		4.4		5.7
	tr.		4.5		5.6
P$_4$	a-p	3.0	4.0		4.8
	tr.	2.4-3.0	3.4-4.1		4.0-4.7
M$_1$	a-p	3.1	3.5		4.2
	tr.	3.6-3.6	4.3-3.9		5.0-5.3
M$_2$	a-p	3.5	3.5	3.5	4.6
	tr.	3.9-3.8	4.5-4.2	4.5-4.2	5.7-5.5
M$_3$	a-p	4.0	4.2		6.1
	tr.	4.0-3.4	4.6-4.0		6.3-5.5

Protospermophilus Gazin

Type species. Citellus (Protospermophilus) quatalensis Gazin.

Emended diagnosis. Skull slightly convex; cranium moderately expanded; dorsal limit of zygomatic plate terminating on side of rostrum; masseteric tubercles small; notches in ventral border of zygomatic plate opposite either M$_1$ or line of contact between P$_4$ and M$_1$; masseteric fossa deeply concave, ending below M$_1$; generally a small pit anterior to masseteric fossa for separate slip of masseter; cheek teeth low crowned but robust; protoconules absent or subordinated in protolophs, metaconules distinct; protocone-posterior cingulum union expanded; entoconid a distinct cusp; entoconid corner angular.

Range. Early Miocene to early Pliocene of western North America.

The genus *Protospermophilus* first appears in the early Miocene of the Great Basin and Great Plains areas and persists through

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[1] The measurements given for *M. monax* represent the mean measurements taken from a sample of 20 specimens.

to the early Pliocene of the Mohave-Sonoran region. Judging from the scattered occurrences previously recorded and the new forms described below, it appears to have been widespread over much of western North America during this time, about as *Citellus* is today. *Protospermophilus* probably formed a separate evolutionary line that, despite its name, had nothing to do with the modern spermophiles after the late Oligocene. There is a strong possibility, however, that the marmots may have evolved from this group sometime in the mid-Miocene.

Structurally, *Protospermophilus* possesses a combination of features that tend to set it off from other sciurids. It shares the development of cheek pouches, the shallow diastema, and slight convexity of the skull with *Citellus,* but in combination with these characters are the robust rostrum, deep incisors, and heavy, crushing dentition, which are more characteristic of *Sciurus*. The dentition is at least superficially somewhat like that of *Sciurus,* with robust, crushing teeth rather than the more lophodont type of dentition seen in *Citellus, Cynomys,* and to a lesser degree in *Marmota*.

PROTOSPERMOPHILUS VORTMANI (Cope)

Plate 12, figure 1

Sciurus vortmani Cope, 1879, p. 1.
Prosciurus vortmani Matthew, 1909, p. 107.
Sciurus vortmani Bryant, 1945, p. 343.

Type. A.M.N.H. No. 6960, a left mandible lacking the anterior portion of the jaw, coronoid, condyle, and angle.

Hypodigm. Type and U.C.M.P. No. 39000, right mandible lacking anterior tip of jaw, ascending ramus, angle and M_2-M_3.

Horizon and locality. *Diceratherium* Beds, John Day Formation, early Miocene. John Day Basin, Oregon.

Diagnosis. Smallest species of genus; mandible short, relatively stout; diastema heavier than in *Miospermophilus;* no crescentic scar anterior to masseteric fossa; entoconids small; postero-lingual corners slightly rounded; no ectostylid or mesoconid; lingual margin elevated into ridge; no distinct mesostylid.

Description. The jaw is of approximately the same size and proportions as that of *Protospermophilus angusticeps* except that it is not quite as robust nor as deep. The diastemal depression is shallow. The masseteric fossa is deep, rounded anteriorly, and terminates below the anterior half of M_1. Both upper and lower borders are marked by well developed ridges. The coronoid process arises at the posterior end of M_2. The mental foramen lies just anterior to P_4 and about halfway down the side of the diastema. U.C.M.P. No. 39000 is somewhat smaller than the type but it is certainly within the normal range of variation.

The incisor is extremely compressed. Its buccal margin is convex rather than flat as is generally the case in *Sciurus*. The cheek teeth increase in size from P_4 to M_3. The anterior portion of the premolar is damaged on the type but preserved on U.C.M.P. No. 39000. The protoconid and metaconid are not as closely appressed as in the later species of the genus. A small anteroconid is present on P_4 but absent on M_1 where the anterior cingulum is small. There is no indication of a mesoconid or ectostylid on P_4-M_3. The ectolophid is not deeply recessed and the buccal valley is consequently shallow. M_1 and M_2 are rhomboidal with small entoconids and somewhat rounded postero-lingual borders. There is a small mesostylid on M_1-M_2. The lingual border of M_3 tapers gradually from the metaconid to the hypoconid, giving the crown a triangular outline.

Discussion. Protospermophilus vortmani is quite far removed from other sciurids known from the early Miocene with the possible exception of the material from Martin Canyon Quarry A in northeastern Colorado. The dentition is closer to that of *Miospermophilus* than to any other contemporary form, but, even here, there are important differences, such as the presence of a low posterolophid and of a distinct entoconid in *P. vortmani*. Also, the structure of the mandible is quite different, that of *P. vortmani* being much heavier, especially through the diastemal area. *P. vortmani* is closely related to *P. kelloggi* of the early Hemingfordian and probably also to the few specimens from Quarry A. It seems quite likley that *P. vortmani* is close to the point of origin of the genus, which probably arose sometime in the late Oligocene.

Measurements

A.M.N.H. No. 6960

Alveolar length P_4-M_3		10.4
Depth below M_1		approx. 8.5
	a-p	tr.
P_4	2.40	2.10-2.50
M_1	2.40	— -2.80
M_2	2.50	— —
M_3	2.80	2.90-2.20

U.C.M.P. No. 39000		
Alveolar length P_4-M_3		10.2
Depth below M_1		8.2
	a-p	tr.
P_4	2.20	2.00-2.20
M_1	2.30	2.40-2.60

PROTOSPERMOPHILUS sp.

Plate 12, figure 2

Sciurus sp. A Wilson, 1960, p. 62.

Referred specimens. K.U. Nos. 10163 LdP^4, 10164 LdP^4, 10165 RM$^{1 \text{ or } 2}$, 10166 RM$^{1 \text{ or } 2}$, 10167 LI$_1$, 10168 RM$_{1 \text{ or } 2}$, 10169 LM$_3$.

Horizon and locality. Pawnee Creek Formation, Arikareean early Miocene. Martin Canyon Quarry A, NW1/4, S.27, T.11N., R.53W., Logan County, Colorado.

Description. The deciduous upper premolars are triangular in occlusal outline due to the presence of a large parastyle. They closely resemble the deciduous premolars of *P. kelloggi* although the protoloph and metaloph are not as high. They also differ from those of *P. kelloggi* in having a small loph running lingually for a short distance from the large mesostyle. The upper first and/or second molars are quadrate with a large protocone and a small bulbous expansion at the point where the posterior cingulum joins the protocone. This is characteristic of all later members of the genus. The protoloph and metaloph are lower than in later forms and there is only a faint indication of the metaconule. The mesostyle is small.

The lower incisor is compressed and bears many fine striations on its anterior face. In this respect it is similar to the lower incisors of *Miospermophilus*, as well as to the later species of *Protospermophilus*. It is flattened medially and conxex laterally. $M_{1 \text{ or } 2}$ is much wider than long and the talonid basin is faintly rugose, characters which are again generally typical for *Protospermophilus*. The entoconid is a distinct cusp connected through a low, uninterrupted posterolophid to the hypoconid. The entoconid is separated from the mesostylid by a shallow notch. Whether an anteroconid was present cannot be determined due to the advanced stage of wear but, if present, it was small. The buccal valley is shallow and the ectolophid poorly developed. The entoconid and posterolophid of M_3 are enlarged as in *P. kelloggi*. There is a large mesoconid that fills the buccal valley.

Discussion. This material from northeastern Colorado, although suggestive of *Protospermophilus,* is too incomplete for specific determination. It is similar to *P. kelloggi* in many ways, especially in the structure of the lower molars and in the structure of the lingual portion of the first and second upper molars. It differs from other species of *Protospermophilus* in the very low lophs of the upper molars. However, upper teeth are unknown for *P. vortmani* so that comparisons can not be made with the only other early Miocene species of the genus. However, it is to be expected that the lophs would be low in the early members of the genus since this was undoubtedly the condition in the ancestral members of the family. Although the material is too poor for a definite statement, I feel it is highly likely that this population will prove to be ancestral to *P. kelloggi* when further specimens are available.

Measurements

		a-p	tr.
K.U. No. 10163	dP^4	2.50	2.30
K.U. No. 10164	dP^4	2.30	2.25
K.U. No. 10165	M$^{1\text{ or }2.}$	2.40	2.80
K.U. No. 10166	M$^{1\text{ or }2.}$	2.40	2.80
K.U. No. 10167	I$_1$	4.25	2.00
K.U. No. 10168	M$_{1\text{ or }2.}$	2.50	3.00-3.00
K.U. No. 10169	M$_3$	3.50	3.40-2.90

PROTOSPERMOPHILUS KELLOGGI[1] n. sp.

Figures 4, 5

Type. A.C. No. 11830 RM$_{1\text{ or }2}$.

Hypodigm. Type and U.W. No. 1415 LdP^4, A.C. No. 10581 RdP^4, C.N.H.M. PM2183 RdP^4, A.C. Nos. 11828 RP^4, 10566 LP^4, 10567 LP^4 and RP^4, C.N.H.M. PM2184 LP^4, PM2185 three RP^4, PM2186 LP^4, PM2200 RP^4, PM2201 RP^4, PM2202 RP^4, U.W. No. 1426 RP^4, A.C. Nos. 10573 LM$^{1\text{ or }2}$, 10574 two LM$^{1\text{ or }2}$, 10575 LM$^{1\text{ or }2}$, 10576 RM$^{1\text{ or }2}$, 10577 two RM$^{1\text{ or }2}$, and two LM$^{1\text{ or }2}$, 10578 LM$^{1\text{ or }2}$, 10579 RM$^{1\text{ or }2}$ and LM$^{1\text{ or }2}$, 10583 RM$^{1\text{ or }2}$, 11287 RM$^{1\text{ or }2}$ and LM$^{1\text{ or }2}$, 11289 two LM$^{1\text{ or }2}$ and RM$^{1\text{ or }2}$, 11290 LM$^{1\text{ or }2}$, 10572 two LM$^{1\text{ or }2}$ and two RM$^{1\text{ or }2}$, 10580 RM$^{1\text{ or }2}$ and two LM$^{1\text{ or }2}$, C.N.H.M. PM2206 four LM$^{1\text{ or }2}$, PM2207 six RM$^{1\text{ or }2}$, PM2187 LM$^{1\text{ or }2}$, U.W. Nos. 1419 LM$^{1\text{ or }2}$, 1420 LM$^{1\text{ or }2}$,

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[1] Named for Rufus B. Kellogg founder of the Kellogg Fellowship at Amherst College.

1421 RM$^{1 \text{ or } 2}$, 1422 LM$^{1 \text{ or } 2}$, 1423 eight RM$^{1 \text{ or } 2}$, 1428 four LM$^{1 \text{ or } 2}$, 1435 RM$^{1 \text{ or } 2}$, A.C. No. 10568 LM^3, 10569 LM^3, 10570 LM^3, 10571 LM^3, 11829 RM^3, 11288 two LM^3, C.N.H.M. PM2188 RM^3, PM2189 LM^3, PM2208 RM^3, PM2209 LM^3, U.W. Nos. 1424 RM^3, 1425 RM^3, A.C. Nos. 10586 LdP$_4$, 10585 LdP$_4$, U.W. No. 1429 LdP$_4$, A.C. Nos. 10582 two RP$_4$, 10585 LP$_4$ and two RP$_4$, C.N.H.M. PM2190 RP$_4$, PM2191 RP$_4$, PM2192 RP$_4$, PM2193 LP$_4$, PM2203 RP$_4$, U.W. Nos. 1416 RP$_4$, 1430 two RP$_4$, A.C. Nos. 10590 two RM$_{1 \text{ or } 2}$, 11831 RM$_{1 \text{ or } 2}$, 11832 LM$_{1 \text{ or } 2}$ and RM$_{1 \text{ or } 2}$, 10589 LM$_{1 \text{ or } 2}$ and RM$_{1 \text{ or } 2}$, 11292 LM$_{1 \text{ or } 2}$ and three RM$_{1 \text{ or } 2}$, 11830 RM$_{1 \text{ or } 2}$, 11835 LM$_{1 \text{ or } 2}$, C.N.H.M. PM2194 LM$_{1 \text{ or } 2}$, PM2195 RM$_{1 \text{ or } 2}$, PM2196 LM$_{1 \text{ or } 2}$, PM2197 LM$_{1 \text{ or } 2}$, PM2210 RM$_{1 \text{ or } 2}$, U.W. Nos. 1417 LM$_{1 \text{ or } 2}$, 1418 LM$_{1 \text{ or } 2}$, 1431 five RM$_{1 \text{ or } 2}$, 1432 six LM$_{1 \text{ or } 2}$, 1433 two RM$_{1 \text{ or } 2}$, A.C. Nos. 11291 two LM$_3$, 11833 two RM$_3$, 10588 RM$_3$ and three LM$_3$, 10584 LM$_3$ and two RM$_3$, C.N.H.M. PM2198 RM$_3$, PM2199 RM$_3$, PM2204 LM$_3$, PM2205 LM$_3$, PM2211 RM$_3$, PM2212 two LM$_3$, U.W. No. 1427 LM$_3$.

Horizon and locality. Split Rock Formation, early Hemingfordian Middle Miocene. Seven miles northwest of Three Forks, Wyoming, south of U.S. 287, S.36, T.29N., R.90W., Fremont County, Wyoming.

Diagnosis. Larger than *Protospermophilus vortmani,* smaller than *P. angusticeps;* dentition not as heavy as in *P. angusticeps, malheurensis,* and *quatalensis;* anterior cingulum small on P^4; indentation slight between protocone and posterior cingulum on M^1-M^2; metaconule generally present on M^3; ectolophid prominent; mesoconid present; entoconid large and distinct; metalophid weak.

Description. The cheek teeth increase in size from P$^4_4$-M$^3_3$. The anterior cingulum of P^4 is very small and subject to obliteration by wear. On dP^4, however, the anterior cingulum and parastyle are well developed. The anterior cingulum of the molars is wide and carries a large parastyle. The protoloph is complete on all cheek teeth and shows only a faint trace of a protoconule on a few of the first and second molars. The metaloph is constricted and the metaconule large on P^4-M^2. On M^3 the metaconule is variably developed but usually present. A faint indentation of the protocone occurs on some of the molars at the point where the posterior cingulum joins it. The mesostyle is small but present on all teeth.

The protoconid and metaconid of P$_4$ are practically fused into one cusp. There is no indication of a trigonid basin, nor of an anteroconid. The hypoconid and entoconid are large and connected by an elevated posterolophid. The mesostylid is small. The ectolophid is set well back from the buccal margin. The deciduous premolars differ primarily in being more cuspate, a strong anteroconid being present together with a large mesostylid and mesoconid.

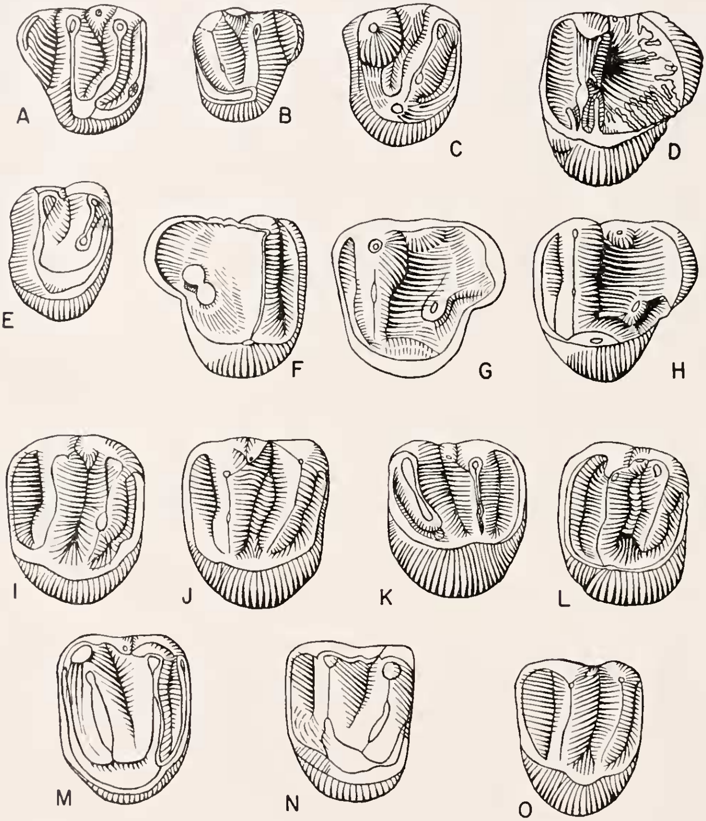

Figure 4. Upper teeth of *Protospermophilus kelloggi* n. sp., x10. *A*, U. W. No. 1415, LdP^4. *B*, C.N.H.M. PM2183, RdP^4. *C*, A.C. No. 10566, LP^4. *D*, A.C. No. 10568, LM^3. *E*, A.C. No. 10567, LP^4. *F*, A.C. No. 10569, RM^3. *G*, A.C. No. 10570, LM^3. *H*, A.C. No. 10571, LM^3. *I*, U.W. No. 1419, LM$^{1 \text{ or } 2}$. *J*, C.N.H.M. PM2187, LM$^{1 \text{ or } 2}$. *K*, A.C. No. 11287, RM$^{1 \text{ or } 2}$. *L*, U.W. No. 1420, LM$^{1 \text{ or } 2}$. *M*, U.W. No. 1421, RM$^{1 \text{ or } 2}$. *N*, A.C. No. 10573, LM$^{1 \text{ or } 2}$. *O*, A.C. No. 10572, LM$^{1 \text{ or } 2}$. (Anterior end to left except for *B*, *F*, *K*, and *M*.)

The first molars are rather square with a greater length in proportion to their width than is the case for the second molars which are more greatly compressed anteroposteriorly. Except for these differences in shape, the first and second lower molars are identical. The anterior cingulum bears little trace of an anteroconid. The trigonid basin is usually open into and not much higher than the talonid basin. The ectolophid is set well back and the mesoconid is either absent or small. The posterolophid is

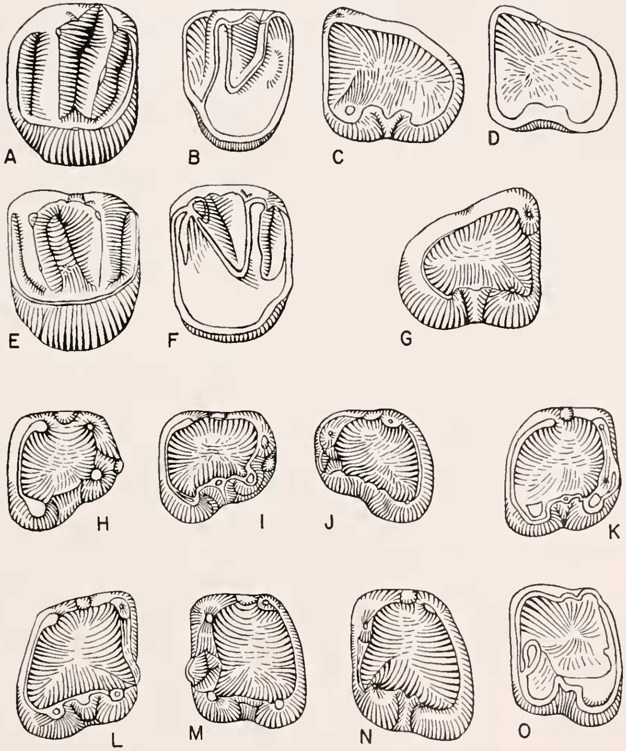

Figure 5. Upper and lower teeth of *Protospermophilus kelloggi* n. sp., x10. *A,* A.C. No. 10578, $LM^{1 \text{ or } 2}$. *B,* U.W. No. 1422, $LM^{1 \text{ or } 2}$. *C,* A.C. No. 10584, LM_3. *D,* U.W. No. 1427, LM_3. *E,* A.C. No. 10583, $RM^{1 \text{ or } 2}$. *F,* U.W. No. 1435, $RM^{1 \text{ or } 2}$. *G,* A.C. No. 11833, RM_3. *H,* A.C. No. 10582, RP_4. *I,* C.N.H.M. PM2190, RP_4. *J,* U.W. No. 1429, LdP_4. *K,* Type, A.C. No. 11830, $RM_{1 \text{ or } 2}$. *L,* A.C. No. 11831, $RM_{1 \text{ or } 2}$. *M,* U.W. No. 1418, $LM_{1 \text{ or } 2}$. *N,* U.W. No. 1417, $LM_{1 \text{ or } 2}$. *O,* A.C. No. 11832, $LM_{1 \text{ or } 2}$. (Anterior end to left except for *E, F, G, H, I, K,* and *L.*)

elevated and crescentic in shape, joining the hypoconid to the large entoconid. The mesostylid is generally small. M_3 resembles the first and second molars except that the hypoconid and posterolophid are greatly expanded, making the tooth longer than wide. The entoconid remains a distinct cusp within this expansion, giving the posterointernal corner of the tooth an angular appearance.

Discussion. P. kelloggi was probably descended from the protospermophile population of Quarry A but too little is known of the Quarry A species to document this change at present. *P. kelloggi* was almost certainly ancestral to *P. angusticeps* of the Deep River, the larger size and greater robustness of the dentition of *P. angusticeps* being the only differences between the two species. There are also some resemblances between *P. kelloggi* and *P. oregonensis* and the latter was either evolved from *P. kelloggi* or *P. angusticeps.*

Measurements

		N	M	S	V	SR
dP^4	a-p	2	2.19			
	tr.	2	2.19			
P^4	a-p	6	1.96	.09	4.64	1.96 ± .27
	tr.	6	2.40	.05	1.95	2.40 ± .15
$M^{1\ \mathrm{and}\ 2}$	a-p	48	2.35	.13	5.36	2.35 ± .39
	tr.	48	2.88	.13	5.20	2.88 ± .45
M^3	a-p	13	2.82	.10	3.65	2.82 ± .30
	tr.	13	2.81	.16	5.52	2.81 ± .48
dP_4	a-p	3	2.18			
	tr.	3	2.02			
P_4	a-p	13	2.17	.09	4.15	2.17 ± .27
	tr.	13	7.69	.10	5.91	1.69 ± .30
$M_{1\ \mathrm{and}\ 2}$	a-p	51	2.29	.11	4.80	2.29 ± .33
	tr.	51	2.58	.23	8.90	2.58 ± .69
M_3	a-p	18	2.79	.15	5.37	2.79 ± .45
	tr.	18	2.63	.13	4.94	2.63 ± .39

PROTOSPERMOPHILUS ANGUSTICEPS (Matthew)

Plate 13, figure 1

Sciurus angusticeps Matthew, *in* Matthew and Mook, 1933, p. 4.
Protospermophilus angusticeps Bryant, 1945, p. 349; Black, 1961b, p. 5.

Type. A.M.N.H. No. 21336, a well preserved skull.

Hypodigm. Type and A.M.N.H. No. 21331, a left maxilla with

P^4-M^3 and a partial right mandible with P_4-M_3; Y.P.M. Nos. 14029, a partial left maxilla with M^3, 14030 a partial left maxilla with M^1-M^2, 14031 a partial left mandible with M_1-M_3, 14032 a partial left mandible with M_1-M_3, 14033 a partial left mandible with M_1-M_2, and 14034 a partial left mandible with M_1.

Horizon and locality. Deep River Formation, Upper Hemingfordian, late Middle Miocene. In the vicinity of Fort Logan, Montana.

Diagnosis. Larger than *Protospermophilus quatalensis,* about equal in size to *P. malheurensis;* skull profile more convex and cranium deeper than in either; rostrum shallower but broader than in *P. malheurensis;* ridges on premaxillae lateral to incisors not prominent; teeth larger, more robust than in *P. kelloggi* or *P. malheurensis;* mandible deeper than in *P. quatalensis;* talonid basins rugose when unworn.

Description. In lateral view the skull roof is gently convex from the tip of the snout, resembling that of *Citellus* in general contour and size. There is a slight concavity at the level of the orbits breaking the outline, but this is not as pronounced as in *Cynomys.* In dorsal view the skull is constricted between the orbits. The cranium is only moderately inflated, lacking almost entirely the inflation medial to and below the posterior zygomatic root. The postorbital bar is missing. The zygomatic arch, although crushed, does not appear to have been as greatly bowed outward as in *Cynomys* and *Citellus,* being more nearly parallel as in *Sciurus.* However, it was apparently somewhat twisted, so that the original medial surface faced upward as it does in the Recent *Cynomys* and *Citellus.* The temporal ridges are extremely weak and fail to meet the occiput.

The contact between the nasals, premaxillae and frontals forms an almost straight line across the dorsal surface just in front of the orbits. The nasals are slender and the premaxillae greatly expanded at this contact. However, anteriorly the nasals form the complete dorsal surface of the rostrum in contrast to the condition seen in *Protospermophilus quatalensis.* The maxillae are excluded from the dorsal surface due to the expansion of the premaxillae. Laterally, there are no prominent ridges on the premaxillae marking the course of the upper incisors. At the level of the superior margin of the infraorbital foramen the premaxillary-maxillary sutures bend posteriorly for a short distance and then turn ventrally. When they reach the ventral surface, they turn anteriorly to join the incisive foramina. There are small pits anterior to the incisive foramen and just posterior to the incisors that appear to indicate the presence of cheek pouches. The masseteric fossae extend forward onto the premaxillae, and the dorsal margins of the fossae are marked by slightly raised ridges lateral to the incisors. The zygomatic notch is opposite the contact between P^4 and M^1. The masseteric tubercle is rather small and situated almost directly below the infraorbital foramen. The infraorbital foramen is vertical and compressed to a narrow slit.

The exact relationships of the tooth rows can not be determined, but they would appear to have converged slightly posteriorly. The pterygoid plates are missing and the size of the pterygoid fossa can not be ascertained. It is also impossible to gain any information concerning the orbital or basicranial foramina. The bullae are small, with their long axis directed anteroposteriorly, and somewhat compressed laterally. There are two transbullar septa. The occipital surface is vertical with a median ridge flanked by narrow depressions running vertically from the top of the skull to the foramen magnum. The foramen magnum is vaguely triangular in outline due to its expanded superior border. The occipital condyles lie at the inferior corners of this triangle and do not expand up the lateral margins.

The diastema, ascending ramus, and angle are not preserved on the five specimens referable to this species. Anteriorly, the masseteric fossa is pointed, with a small crescent-shaped depression at its termination below the anterior end of M_1. This depression undoubtedly received a separate slip of the masseter which was beginning its migration onto the rostrum above. The fossa is deep with prominent ridges above and below. From what little is left of the diastemal area, it would appear that the mandible sloped downward gently from P_4, as in *P. vortmani*, rather than dropping off abruptly as in *Protosciurus* and *Sciurus*. The jaws are more robust than those of *Miospermophilus*.

The upper dentition, although not high crowned, is extremely heavy and robust. The upper incisors are strongly recurved and the enamel on their anterior face is finely wrinkled. There is also one shallow groove running down the middle to the anterior face. P^3 is represented only by large alveoli. P^4 is much smaller than the molars but is similar to them in pattern. The protocone is broad and elevated above the lophs and cingula. The anterior cingulum is narrow and bears only a small parastyle at its buccal end. The protoloph passes straight across the tooth to the protocone, while the metaloph joins the protocone at a distinct angle and is constricted at this union. There is no indication of a protoconule, and the metaconule is small. The posterior cingulum is wide lingually but narrows rapidly and fails to reach the buccal margin. M^1 and M^2 are identical in pattern, varying only slightly in their occlusal outlines, M^2 being somewhat wider in relation to its length. The anterior cingula are broad and carry high parastyles on their buccal margins. The lophs are heavy with little indication of conules, and the metaloph is constricted at its junction with the protocone. There is an expansion at the posterointernal corner of the teeth where the posterior cingulum joins the protocone. However, the indentation at this point is not as strong as that present in *P. malheurensis* and *P. quatalensis*. There is a distinct mesostyle on all three molars. M^3 is slightly larger than M^2, due to the expansion of the posterior half of the tooth; this section is sharply constricted and set off from the protocone. There is no indication of a metaconule such as is sometimes found in *P. kelloggi*.

The lower dentition gives the same impression of heaviness as does the upper, and when unworn, the talonid basins are rather rugose, the rugosity disappearing rapidly with wear. The cheek teeth increase in size from P_4 to M_3. The only lower fourth premolar preserved is well worn with most of the pattern consequently obliterated. The protoconid and metaconid are closely appressed and there is no trace of an anteroconid. M_1 is generally somewhat squarer in occlusal outline than is M_2, which is considerably wider than long. On both teeth the trigonid basins are not greatly elevated above the talonids, from which they are isolated by a short metalophid that merges into the base of the high metaconid. The trigonid basins are bounded anteriorly by distinct, bulbous cingula. In all cases the entoconids are distinct cusps and are joined to the hypoconids through uninterrupted posterolophids. The ectolophids are set well back from the buccal margins and generally bear rather large mesoconids. The mesostylids are prominent and are set off from the entoconids by shallow valleys. M_3 varies considerably in occlusal outline with wear. When unworn, the posterointernal area is expanded, giving the tooth a somewhat rectangular appearance. As wear proceeds, the outline becomes more and more triangular through a reduction of the width of the posterior half of the tooth. There is no distinct trigonid basin on M_3 nor is there any indication of an anteroconid.

Discussion. The crushing dentition of *P. angusticeps* is as advanced as any known in the genus, comparable to that of *P. quatalensis* and surpassing that of *P. malheurensis*. The same is also true for the zygomasseteric structure, which is as advanced in *P. angusticeps* as in later species. *P. angusticeps* could not have given rise to *P. malheurensis* because of the great discrepancy in the size of the teeth in relation to overall skull size in the latter. It is highly unlikely that *P. angusticeps* was ancestral to *P. quatalensis* for the same reason. There are some resemblances between *P. angusticeps* and *P. oregonensis* of the Great Basin, however, and the later species was probably descended from a Great Plains species, very possibly *P. angusticeps.* There are no members of the genus known after the Middle Miocene in the Great Plains and it is probable that as the region became more arid and the grasslands expanded a large share of the food supply for the group was removed, with the subsequent extinction of *Protospermophilus* in this area.

Measurements

A.M.N.H. No. 21336

Length of skull	59.3
Depth of rostrum at anterior end of zygomatic plate	14.5
Width of rostrum at anterior end of zygomatic plate	12.2
Width of skull at postorbital notch	approx. 13.5
Width of skull behind posterior zygomatic root	approx. 23.0
Length of palate	27.5
Alveolar length P^3-M^3	approx. 12.0

A.M.N.H. No. 21331

Alveolar length P^3-M^3	approx. 10.8
Depth of mandible below M_1	8.1

		N	M
P^4	a-p	3	2.30
	tr.	3	2.90
M^1	a-p	4	2.60
	tr.	4	3.20
M^2	a-p	3	2.70
	tr.	3	3.33
M^3	a-p	2	2.80
	tr.	2	2.95

P_4	a-p	1	2.20
	tr.	1	2.00-2.30
M_1	a-p	5	2.54
	tr.	5	2.74-3.02
M_2	a-p	4	2.82
	tr.	4	3.08-3.15
M_3	a-p	3	3.00
	tr.	3	2.93-2.60

PROTOSPERMOPHILUS OREGONENSIS (Downs)

Plate 13, figure 2; Plate 14, figure 1

Arctomyoides oregonensis Downs, 1956, p. 217.

Type. U.C.M.P. No. 39093 left mandibular ramus without coronoid and condylar processes.

Hypodigm. Type and U.C.M.P. No. 40241 left P_4.

Horizon and locality. Late Hemingfordian or early Barstovian, middle to late Miocene. SE ¼ of NE ¼, S. 15, T.12S., R.25E., Wheeler County, Oregon.

Emended diagnosis. Largest species of genus; length of diastema in relation to alveolar length greater than in other protospermophiles; ectolophid moderately developed; mesoconid large; large anteroconid on M_1-M_2; anteroposterior compression of M_1-M_2 greater than in any other species of the genus.

Description. The mandibular ramus is shallow and thin in relation to its overall length. The diastema is long, dropping gently from P_4, and the diastemal depression is shallow. The mental foramen lies just below the diastemal level midway between P_4 and the incisor. The masseteric fossa ends below the anterior root of M_1 and is rounded anteriorly. The jaw is crushed in this region but the fossa was evidently deeply concave. The angle is not twisted medially but lies in the vertical plane of the ramus. The ascending ramus rises steeply opposite hypoconid of M_2.

The incisor is greatly compressed and flattened both laterally and medially. P_4-M_3 are only moderately worn, and the talonid basins are all rugose. The protoconid and metaconid are closely appressed on P_4 with a minute anteroconid present on the protoconid slope. The ectolophid is moderately strong and bears a small mesoconid. The posterolophid is low and passes almost straight across P_4 to the entoconid. A small mesostylid is present lingually. The molars are nearly identical in structure. They increase in size from M_1 to M_3 with M_3 having a greatly expanded hypoconid and heavy expanded posterolophid. Strong anteroconids, moderately developed ectolophids, and mesoconids are present on M_1-M_3. The trigonid basin is enclosed on M_1-M_2 by a heavy metalophid. On M_3 the trigonid basin is open with the metalophid passing into the talonid basin. Small mesostylids are present on M_1-M_2 but absent on M_3. The posterolophids on M_1-M_2 are low and curve anteriorly to the entoconids. The teeth are consequently much narrower lingually than buccally.

Discussion. Downs (1956, pp. 217-222) in discussing the relationships of *Protospermophilus oregonensis* believed that it showed a greater resemblance to *Arctomyoides arctomyoides* than to any other Miocene sciurid. At that time he was able to examine *Palaearctomys "macrorhinus"* which he assumed from Bryant's (1945) earlier work was closely related, possibly congeneric with *Arctomyoides,* but he did not examine *Arctomyoides arctomyoides.* As I have pointed out above (p. 153) *Arctomyoides* is probably only distantly related to *Palaearctomys. Protospermophilus oregonensis* differs from *Arctomyoides arctomyoides* in the following characters: mandible more slender, relatively longer diastema, different position and extent of masseteric fossa (a character which Downs [*op. cit.,* p. 221] pointed out), entirely different proportions of P_4-M_3, presence of strong anteroconids and metalophids on M_1-M_2, and small mesostylids. It is clear that *Protospermophilus oregonensis* is not closely related to *Arctomyoides.*

The characters which distinguish *P. oregonensis* from *Arctomyoides* are precisely those found in the protospermophile group of Tertiary sciurids. *P. oregonensis* is particularly close to *P. angusticeps* from the Deep River, and although larger could certainly have evolved from that species. *P. oregonensis* differs from *P. quatalensis* in its larger and more slender mandible and larger cheek teeth.

P. oregonensis does bear certain resemblances to the earliest known species of *Marmota, M. vetus* (Marsh). These include: general compressed shape of P_4-M_3, strong metalophids on M_1-M_2, well developed ectolophids on P_4-M_3, and the position and shape of the masseteric fossa. *P. oregonensis* differs from *M. vetus* in possession of mesoconids and in its much lower crowned teeth. *P. oregonensis* differs considerably from *Palaearctomys montanus* particularly in the greater anteroposterior compression of M_1-M_2 in *P. oregonensis.* The resemblances between the protospermophiles in general and *P. oregonensis* in particular and such early marmots as *Marmota vetus* and *M. minor* are discussed more fully above (p. 163).

Measurements

U.C.M.P. No. 39093

Length of diastema	10.4
Depth of mandible at mental foramen	6.5
Depth of mandible below M_1	8.7
Alveolar length P_4-M_3	12.5

	a-p	tr.
I_1	3.70	1.60
P_4	2.60	2.30-2.60
M_1	2.90	3.00-3.20
M_2	3.10	3.50-3.50
M_3	3.60	3.50-3.00

U.C.M.P. No. 40241

P_4	2.50	2.30-2.60

PROTOSPERMOPHILUS MALHEURENSIS (Gazin)

Plate 13, figure 3; Plate 14, figure 2

Sciurus malheurensis Gazin, 1932, p. 56.

Protospermophilus malheurensis: Bryant, 1945, p. 347.

Type. L.A.C.M. (C.I.T.) No. 129, a skull lacking the region posterior to the postorbital bar, the nasals, incisors, RP^3, and LP^3-M^1.

Hypodigm. Type and L.A.C.M. (C.I.T.) No. 333, a poorly preserved skull without dentition and rostrum, L.A.C.M. (C.I.T.) Nos. 3077A LM^1, and 3077B RM^1.

Horizon and locality. Late Hemingfordian, late Middle Miocene. 28 miles S. of Harper and 3 mi. NW. of Skull Spring, Malheur County, Oregon. L.A.C.M. (C.I.T.) Nos. 3077A and 3077B from Beatty Butte local fauna, Oregon.

Emended diagnosis. Rostrum deep; skull roof flat; lateral incisor ridges intermediate in development between *P. angusticeps* and *P. quatalensis;* pits posterior to upper incisors deep; cheek teeth small in relation to size of skull.

Description. Of the two skulls, the type, although not as complete, is by far the better preserved. The upper profile is flatter than that of *P. angusticeps,* particularly from the postorbital bar to the occiput. The interorbital width is approximately the same in the two species. The rostrum is narrow and quite deep. The frontal-nasal and frontal-premaxillary sutures are as in *P. angusticeps,* as is the almost total exclusion of the maxillae from the dorsal surface of the skull. The rostral ridges lateral to the incisors are more pronounced than in *P. angusticeps,* but are not as greatly developed as in *P. quatalensis.* In contrast to the condition in *P. angusticeps,* the premaxillary-maxillary suture passes straight down the side of the rostrum until it reaches the palate, where it turns forward to the incisive foramen. The pits just behind the incisors are deep. The masseteric tubercles are low and drawn out from the ventral border of the infraorbital foramen back towards P^3. The infraorbital foramen is slit-like. The zygomatic plate is not appreciably different in area and shape from that of *P. angusticeps.*

Little can be learned concerning the basicranial region due to the poor preservation of L.A.C.M. (C.I.T.) No. 333. It would appear that the pterygoid fossa was relatively large and deep. The ectopterygoid ridge is strong and the lateral pterygoid plate evidently reached the bullae. These are of the same size and shape as those of *P. angusticeps* and also have two septa. The occiput slants slightly posteriorly as in some species of *Citellus,* and has a median ridge flanked by narrow depressions as in *P. angusticeps.* The foramen magnum is ovate and lacks the somewhat expanded superior margin seen in *P. angusticeps.* The condyles differ from those of *P. angusticeps* in being more greatly expanded lateral to the foramen magnum.

In relation to the size of the skull, the teeth are small. The anterior cingulum on P^4 is small with no parastyle, while on M^1-M^3 it is large and carries a high parastyle. The protoloph on P^4-M^3 is complete, passes directly across to the protocone, and shows no trace of a protoconule. The metaloph on P^4-M^2 is constricted at its junction with the protocone, passes obliquely across to the protocone, and shows a distinct metaconule. A large metaconule is also present on M^3. There is a small mesostyle on all the teeth. On P^4-M^2 the posterior cingulum fails to reach the buccal margin and, lingually, joins the protocone at a right angle. At this junction there is a slight expansion marked by a shallow groove on the protocone. The posterior cingulum on M^3 bends sharply buccally from the protocone and then expands posteriorly.

Discussion. There is no record of *Protospermophilus* in the Great Basin between the early Miocene and the late Middle Miocene so that it is difficult to trace the descent of *P. malheurensis.* However, it was probably descended from *P. vortmani* but, as only lower teeth and jaws are known for the latter and upper teeth and skulls for the former, there is no way to determine how great the change between these forms may have been. It is probable that *P. malheurensis* gave rise to *P. quatalensis* of the Barstovian and early Clarendonian.

Measurements

L.A.C.M. (C.I.T.) No. 129

Depth of rostrum at anterior end of zygomatic plate	14.5
Width of rostrum at anterior end of zygomatic plate	11.5
Length of palate	29.0
Width of palate at M^1	8.2
Alveolar length P^3-M^3	10.5

	a-p	tr.
I^1	4.30	2.40
P^4	2.00	2.40
M^1	2.40	2.70
M^2	2.40	2.80
M^3	2.50	2.70

PROTOSPERMOPHILUS QUATALENSIS (Gazin)

Plate 13, figure 4; Plate 15

Citellus (Protospermophilus) quatalensis Gazin, 1930, p. 64.
Protospermophilus quatalensis: Bryant, 1945, p. 350.
Sciurus venturus Bryant, 1945, pp. 345-346.

Type. L.A.C.M. (C.I.T.) No. 30, a partial skull with LP^3-M^2 and RP^4-M^1, and partial right and left mandibles with RM_1-M_2 and LP_4-M_1.

Type of synonym. U.C.M.P. No. 34450, a partial left ramus with M_1-M_3.

Hypodigm. Types and L.A.C.M. (C.I.T.) Nos. 31 a partial left mandible with P_4-M_2, and 32 a partial left mandible with P_4-M_3.

Horizon and locality. Upper Barstovian, late Miocene. Quatal Canyon, 8 mi. E. of Cuyama Valley, Ventura County, California. U.C.M.P. No. 34450, Clarendonian, early Pliocene, N. side of Apache Canyon, 8 mi. NE of Cuyama Valley, S.2, T.8N., R.23W., Ventura County, California.

Emended diagnosis. Size of *P. malheurensis;* rostrum broad, short, relatively shallow; premaxillae with dorsal expansion to tip of snout; ridges lateral to incisors heavy; mandibles shallow below P_4-M_3; cheek teeth small in relation to skull size; notch between protocone and posterior cingulum deep on M^1; lingual border of P^4-M^2 straight due to well developed cusp-like expansion at lingual end of posterior cingulum; ectolophids weak; no mesostylid on lower molars.

Discussion. Bryant (*op. cit.,* p. 346) described a mandible from the early Pliocene Cuyama fauna as a new species of *Sciurus, S. venturus.* He did not compare it with *Protospermophilus quatalensis* but it appears almost identical to that species. The mandible is somewhat heavier and deeper but the low, heavy posterolophids, almost complete submergence of the entoconid, and the heavy dentition all indicate relationship with *Protospermophilus* rather than *Sciurus.*

Description. The skull roof is crushed, and missing behind the orbits with the premaxillae riding over the nasals. The lateral and ventral relationships of the premaxillae and maxillae have not been distorted. Also the dorsal position of the premaxillae appears to be true with a greater expansion onto the top of the rostrum than is known in any other North American sciurid. The ridges on the premaxillae lateral to the incisors are extremely heavy and are confluent with the dorsal edge of the masseteric fossa. The premaxillary-maxillary suture passes straight down the side of the rostrum to the level of the infraorbital foramen where it bends posteriorly towards the masseteric tubercle; it then bends anteriorly to the incisive foramen. The cheek-pouch muscle pits posterior to the incisors are approximately as in *P. malheurensis.* The masseteric fossa terminates anterodorsally on the premaxilla just anterior to the premaxillary-maxillary suture. There is a large, shallow concavity marking the dorsal half of the fossa. The infraorbital foramen lies above the masseteric tubercle, and is rather small and compressed. The masseteric tubercle is large, and there is a well developed muscle scar medial to it which passes anteriorly to the premaxillary-maxillary suture. The notch in the zygomatic plate is opposite the middle of M^1.

The jaw is shallow below the cheek teeth, more so in the Quatal Canyon material than in the Clarendonian specimen, and is unlike any other species of *Protospermophilus* in which the jaw is known. The masseteric fossa is consequently compressed and more acutely angled anteriorly. The small crescentic scar anterior to the main area of the masseteric fossa lies below P_4. The diastema is very shallow and broad and the mental foramen lies just anterior to P_4 almost on the dorsal surface of the diastema.

The upper incisors are strongly recurved and show many fine striations on their anterior faces. P^3 is a minute peg, although on the right side, where it is missing, the alveolus is large. The upper cheek teeth are all nearly square in outline although this was probably not the case of M^3 which is absent on both sides. The lingual border of P^4-M^2 is flat with a large bulbous expansion posterior to the protocone at the point where the posterior cingulum joins the protocone. There is a marked cleft at this point on M^1 but this is not present on P^4 and M^2. The anterior cingulum is rather small on P^4 carrying a small parastyle which would be lost with wear; on M^1-M^2 the anterior cingulum is larger with a high parastyle. The protoloph is complete on P^4-M^2 with no trace of a protoconule; the metaloph is constricted on these teeth and shows a large metaconule. The posterior cingulum is short and displays the large lingual expansion mentioned above. A small mesostyle is present on P^4-M^2.

The lower incisors also show many fine striations on their anterior faces. They are not as deep nor as compressed as in *Sciurus* or *Citellus*, resembling more those of *Marmota*. The lower cheek teeth are small but robust. They all display rather rugose talonid basins. P_4 is much smaller than M_1-M_3. The protoconid and metaconid are distinct but closely appressed. There is no trace of an anteroconid. The posterolophid is continuous, heavy, and of medium height with the entoconid almost completely blended into it. The buccal valley is deep and is dammed internally by a large mesoconid. The ectolophid is weak and the mesostylid absent. M_1 and M_2 are identical in pattern, differing only in size. They both have strong anteroconids, open trigonid basins, weak ectolophids, deep buccal valleys, strong mesoconids, no mesostylids, and wide, heavy posterolophids. (Bryant, *op. cit.*, p. 350, states that mesostylids are present but I can find no trace of them.) M_3 agrees in pattern with the first two molars except that the hypoconid and posterolophid are greatly expanded posteriorly.

Discussion. *P. quatalensis* is the last protospermophile known. There seems to be little doubt but that it was descended from *P. malheurensis*. In the small size of its teeth in relation to skull size it reflects the condition seen in that species and stands in contrast to that of the Great Plains species. It differs from *P. malheurensis* primarily in the structure of the rostrum which is more heavily built than in its ancestor. Part of this massiveness is due to the enlarged incisors and the consequent lateral expansion of the premaxillae. This condition could have been easily reached from that in *P. malheurensis* with the depth of the rostrum decreasing as the premaxillae expanded laterally to accomodate the incisors. The dorsal expansion of the premaxillae onto the top of the rostrum would tend to strengthen the incisor alveoli allowing for greater strain to be placed on them. Only minor changes in the dentition would be necessary to bring *P. malheurensis* to the level of *P. quatalensis.*

Measurements

L.A.C.M. (C.I.T.) No. 30

Length of diastema	6.5
Depth of mandible below mental foramen	6.4
Depth of mandible below M_1	7.0
Alveolar length P^3-M^3	10.3
Alveolar length P_4-M_3	10.2

	a-p	tr.
LP^4	2.30	2.50
LM^1	2.50	2.70
LM^2	2.60	——
RP^4	2.30	2.50
LI_1	3.40	1.90
LP_4	2.20	1.80-2.10
LM_1	2.40	2.40-2.60
RM_1	2.40	2.40-2.50
RM_2	2.70	2.70-2.70

L.A.C.M. (C.I.T.) No. 31

Alveolar length P_4-M_3	10.5

	a-p	tr.
P_4	2.00	1.50-2.00
M_1	2.50	2.40-2.70
M_2	2.70	2.90-3.00

L.A.C.M. (C.I.T.) No. 32

Alveolar length P_4-M_3	10.6

	a-p	tr.
M_1	2.50	2.60-2.80
M_2	2.80	3.00-3.10
M_3	3.20	3.00-2.70

U.C.M.P. No. 34550

	a-p	tr.
M_1	2.60	2.70-2.90
M_2	2.70	3.10-3.10
M_3	3.20	3.10-2.90

MIOSPERMOPHILUS n.gen.

Type species. Palaearctomys? bryanti Wilson.

Diagnosis. Size small; cheek teeth low crowned; protoconules subordinated in protolophs; metaconule small; metaloph slightly constricted at the protocone; protocone partially constricted, not occupying all of the lingual border on M^1-M^2; lower molars rhomboidal, inner half narrower than outer half; posterolophids low; entoconids small; ectolophids set well in from buccal margin; diastema fairly long, diastemal depression shallow; masseteric fossa ending below posterior half of P_4.

Range. Late Arikareean of northeastern Colorado to early Hemingfordian of central Wyoming.

MIOSPERMOPHILUS BRYANTI (Wilson)

Plate 16

Sciurus sp. Galbreath, 1953, p. 98.
Palaearctomys? bryanti Wilson, 1960, p. 57.

Type. K.U. No. 10149, a complete right mandible.

Hypodigm. K.U. Nos. 9290, partial right mandible with P_4, M_2-M_3, 10156 RdP^4, 10155 LP^4, 10157 two $LM^{1 \text{ or } 2}$ and $RM^{1 \text{ or } 2}$, 10158 $RM^{1 \text{ or } 2}$, 10159 $LM^{1 \text{ or } 2}$, 10160 LM^3, 10161 upper incisors, 10162 lower incisors, 10150 LP_4, 10151 RP_4, 10152 LM_2, 10153 RM_2, 10154 LM_3.

Horizon and locality. Pawnee Creek Formation, late Arikareean, early Miocene. Martin Canyon Quarry A, NW. 1/4, S. 27, T.11N., R.53W., Logan County, Colorado.

Diagnosis. Smaller than *M. wyomingensis;* diastemal region of mandible long; diastemal depression shallow; metaloph not as constricted as in that species; lophs low; metaconules small; protocone large; entoconid not completely submerged in posterolophid.

Description. The mandible agrees in most respects with that of *Citellus variegatus.* The diastemal region is long and slender as in *Citellus* and not as massive as that of *Marmota.* The diastemal depression is shallow and the superior border of the mandible curves gently downward from the anterior end of P_4. In *Protosciurus* and *Palaearctomys,* the border drops steeply anterior to P_4. The masseteric fossa ends below the posterior end of P_4 and is somewhat rounded. The coronoid process is long, sharply pointed, and curves backward, its dorsal border paralleling the condylar process, as in spermophiles. In marmots and tree squirrels it is generally shorter, not as slender, and does not curve as far backwards. The articular face of the condyle shows a tendency toward the lateral expansion seen in *Citellus* and *Marmota*, but not in *Sciurus*. The angle is rather blunt and only slightly twisted medially.

The deciduous fourth upper premolar is smaller than P^4. The anterior cingulum is greatly expanded but lies well below the level of the protoloph. The protocone is high and rather sharp, the lophs joining it well down on its external face. The protoloph is low, unconstricted, and shows no sign of a protoconule; the metaloph is constricted and the metaconule is distinct. The posterior cingulum is very small. Buccally, there is a large mesostyle uniting the paracone and metacone. P^4 is quite different from its deciduous predecessor. The anterior cingulum is much narrower and lower, there is no mesostyle, the lophs are sharper and steeper, and the metaconule is only slightly developed.

On M^{1-2} the anterior cingulum is moderately expanded and bears a large parastyle; the posterior cingulum is small. There is a faint metaconule in the metaloph, which is slightly constricted at the protocone; there is no distinct protoconule and the protoloph is unconstricted. A small mesostyle is present. The anterior cingulum is smaller on M^3 than on M^{1-2} and lacks a parastyle. The protoloph is low and complete. There is no trace of a metaconule or of a mesostyle. The posteroexternal portion of M^3 is expanded as in *Citellus*. The upper incisors are extremely compressed and have many fine, interwoven striations running longitudinally on their anterior faces.

The lower dentition is low crowned and rather lightly built. The protoconid and metaconid are closely appressed on P_4 with no trace of an anteroconid. The posterolophid forms a gentle curve from the large hypoconid through an indistinct entoconid to the metaconid. The ectolophid is weak, set well in from the buccal margin, and shows no trace of a mesoconid or ectostylid. M_1 is rather more quadrate than M_2, the anterior and posterior halves of the tooth being more nearly equal in width. The trigonid basin is small, enclosed, and raised only slightly above the level of the talonid basin on M_1 and M_2. The protoconid and hypoconid are of equal size on these teeth. The entoconid is small on both; the posterolophid is somewhat elevated and curves gently through the entoconid. The mesostylid is small and there is no mesoconid or ectostylid. The ectolophid is set well back from the buccal margin. M_3 is the largest cheek tooth, with a large, expanded hypoconid and a posterolophid in which the entoconid is completely subordinated. A small mesoconid is present on the rather weak ectolophid. The lower incisor is extremely compressed, rounded lingually, and has many very fine striations running longitudinally.

Discussion. Wilson (1960), in his discussion of *M. bryanti,* pointed out its many resemblances to the chipmunks but concluded that it was probably more closely allied to *Arctomyoides* and *Palaearctomys,* both of which were placed in close relationship to *Marmota* by Bryant (1945). After a careful examination of the specimens, this suggested relationship seems highly dubious to me. *Arctomyoides* appears to be a highly specialized offshoot of the marmot line and *Palaearctomys,* although somewhat closer to *Marmota,* also possesses certain characters that distinguish it from that genus and from *Miospermophilus.* Wilson (1960, pp. 61-62) opposes assignment of *M. bryanti* to the chipmunks on three counts: "(1) *P.* ? *bryanti* differs from *Eutamias* and *Tamias* in a number of morphological details, such as heaviness of lower jaw and relatively short anteroposterior diameters of molars M^{1-2}_{1-2}; (2) chipmunks may not in themselves be a natural group (White, 1953, p. 560); (3) characters most strongly suggesting assignment of *P.* ? *bryanti* to chipmunks would also suggest chipmunk affinities for several of the European Miocene species and it is hardly likely that these all are chipmunks."

The lower jaw while heavier and deeper than in the modern species of chipmunks is still much more slender than any other sciurid mandible known from the North American Oligocene or Miocene, and this could easily be interpreted as a hold-over from the ancestral paramyine condition. If the specimen is an early spermophile, these morphological differences from, as well as the resemblances to, chipmunks are easily explainable (especially if, as discussed later, p. 234, the spermophiles were descended from a chipmunk-like sciurid). The greater anteroposterior compression of the molars agrees well with the interpretation of this form as an early spermophile. Wilson's second point seems hardly applicable in this instance. Whether or not chipmunks are a natural group, *M. bryanti* does resemble them in many details, and, or so it seems to me, assignment to this group rather than to the marmots would have been more acceptable on the characters available. Wilson's third objection to a chipmunk relationship for this species is perfectly valid; in view of their habitat preferences and their sparse representation in the North American Tertiary, you would not expect a large number of chipmunks in the European record. However, this similarity of *M. bryanti* to European species argues more convincingly for a spermophile relationship than for a marmot relationship. It seems much more likely to me that these European species represent ground squirrels, which are abundantly represented in the North American Tertiary and which are so abundant today.

As Wilson points out there are several features found in *M. bryanti* which are more advanced than they are in *Arctomyoides* or *Palaearctomys.* These include: greater compression and fine striation of the incisor, and less elongation of M_3. These are characters which one would certainly expect in an early spermophile. He emphasizes the small size of the dentition in relationship to jaw size in *M. bryanti* and *Palaearctomys.* The ratio of jaw length to alveolus length in *M. bryanti* is approximately 4.2; in *Palaearctomys* it is 4.4; and in *C. (Otospermophilus) variegatus* and *beechyi* it ranges from 4.0-4.2. *M. bryanti* is, therefore, just as close to the true spermophiles in this respect as it is to *Palaearctomys.* Finally, the fine longitudinal striations on the incisors appear to be an extremely variable character occurring in several sciurid lines, including the true spermophiles.

There are many characters which argue for considering this species to be a true spermophile, in addition to those already mentioned: (1) the metaloph on M^{1-2} is slightly constricted; (2) the protocone is not greatly expanded anteroposteriorly; (3) the lower molars are narrower internally than externally with the entoconid displaced anteriorly; (4) the entoconid is relatively small and a part of the curving posterolophid; and (5) the diastema is relatively long and the diastemal depression shallow. The characters in common between *M. bryanti* and the chipmunks indicate, I believe, that the ground squirrels evolved from chipmunk-like sciurids, probably in the late Oligocene.

Miospermophilus bryanti is close to the point of chipmunk-ground squirrel divergence as its many resemblances to both groups attest. *M. wyomingensis* was undoubtedly descended from *M. bryanti.*

Measurements

K.U. No. 10149	
Length of mandible	31.0
Length of diastema	6.3
Depth of mandible below P_4	6.0
Alveolar length P_4-M_3	7.4

		K.U. 10149	K.U. 9290	Various teeth (from Wilson, 1960)	
I_1	a-p	2.50	2.70	2.60	2.00 (young)
	tr.	1.20	1.30	1.30	1.10
P_4	a-p	1.30	1.40	1.25	1.40
	tr.	— -1.40	1.10-1.50	1.30	1.40
M_1	a-p	1.60	—		
	tr.	1.70-1.80	—		
M_2	a-p	1.70	1.70	1.80	1.80
	tr.	2.00-2.00	2.00-2.00	2.00	2.00
M_3	a-p	2.00	2.00	2.00	2.00
	tr.	2.00-1.60	2.00-1.60	2.00	2.00

		Various teeth (from Wilson, 1960)		
I^1	a-p	3.10	2.70	2.80
	tr.	1.40	1.25	1.40
dP^4	a-p	1.30		
	tr.	1.40		
P^4	a-p	1.40	1.50	
	tr.	1.70	1.80	
M^1	a-p	approx. 1.50	approx. 1.60	
	tr.	2.00	2.00	
M^2	a-p	1.70	1.75	
	tr.	2.20	2.20	
M^3	a-p	2.20		
	tr.	2.10		

MIOSPERMOPHILUS WYOMINGENSIS n. sp.

Figure 6

Type. A.C. No. 10898 LM$_{1 \text{ or } 2}$.

Hypodigm. C.N.H.M. PM2171 RdP^4, PM2183 RdP^4, A.C. Nos. 10895 RP^4, 10899 two LP^4, 10563 LP^4, C.N.H.M. PM2168 LP^4, PM2169 LP^4, U.W. No. 1409 LP^4, A.C. Nos. 10563 LM$^{1 \text{ or } 2}$, 10896 RM$^{1 \text{ or } 2}$, 10897 RM$^{1 \text{ or } 2}$, 10564 LM$^{1 \text{ or } 2}$, C.N.H.M. PM2170 RM$^{1 \text{ or } 2}$, PM2172 LM$^{1 \text{ or } 2}$, PM2173 RM$^{1 \text{ or } 2}$, U.W. Nos. 1407 RM$^{1 \text{ or } 2}$, 1408 RM$^{1 \text{ or } 2}$, 1411 LM$^{1 \text{ or } 2}$, C.N.H.M. PM2174 LM^3, U.W. Nos. 1410 RM^3, 1412 RM^3, C.N.H.M. PM2178 LdP$_4$, PM2179 LdP$_4$, PM2213 RP$_4$, PM2175 LP$_4$, A.C. Nos. 10565 two RM$_{1 \text{ or } 2}$, 11286 LM$_{1 \text{ or } 2}$, C.N.H.M. PM2176 LM$_{1 \text{ or } 2}$, PM2177 LM$_{1 \text{ or } 2}$, U.W. Nos. 1413 LM$_{1 \text{ or } 2}$, 1414 RM$_{1 \text{ or } 2}$, C.N.H.M. PM2180 LM$_3$, PM2181 LM$_3$, PM2182 RM$_3$.

Horizon and locality. Split Rock Formation, early Hemingfordian, Middle Miocene. Seven miles northwest of Three Forks Wyoming, south of U.S. 287, S. 36, T.29N., R.90W., Fremont County, Wyoming.

Diagnosis. Larger than *M. bryanti;* lophs higher and sharper; protocone not filling lingual margin; metaconules very distinct; metaloph greatly constricted; entoconid incorporated in posterolophid; entoconid region angulate; posterointernal part of M_3 partially expanded.

Description. The subquadrate P^4 is smaller than the molars. The protoloph and metaloph converge towards the protocone where the metaloph is sharply constricted. The anterior cingulum is small, bending abruptly posteriorly to join the protocone. The posterior cingulum terminates below the metacone, not passing to the buccal side of the tooth, and rises gradually to join the protocone without a sharp bend. The protoconule is not visible as a separate component of the protoloph. The mesostyle is small.

The deciduous fourth upper premolars are slightly smaller than the permanent teeth. The anterior cingulum is restricted to the buccal half of the tooth and is a small flat shelf. The posterior cingulum is very small and rises gently to join the protocone. The metaloph is constricted at its junction with the protocone and the metaconule is distinct.

It is impossible to separate upper first and second molars, and the description given here applies to both. The teeth are generally triangular to subquadrate in outline. There is no indication of any division of the protocone into two cusps. The lophs and cusps are relatively sharp and the trigon is V-shaped. The metaconules are generally distinct cusps. The protoloph joins the protocone at a right angle to the anteroposterior axis of the tooth while the metaloph passes slightly anteriorly to join the protocone. The metaloph is usually constricted at the protocone. The anterior cingulum is moderately developed and somewhat higher than the posterior cingulum. The anterior cingulum changes direction abruptly at the protocone, joining it at a right angle while the posterior cingulum rises to the protocone in a gentle curve. There is usually a small mesostyle on all the teeth.

The third upper molars are approximately as long as they are wide and are triangular in occlusal outline. The paracone is the highest cusp with the protocone and metacone about equal in height. The protocone is swollen and fills the lingual portion of the tooth with the posterior cingulum bending sharply posteriorly and buccally. The anterior cingulum is well developed, rising steeply to join the paracone, and it is lower than the protoloph. The metacone is swollen and occupies the whole posterointernal corner of the tooth. There is no mesostyle.

The length of the fourth lower premolars is approximately equal to their posterior width. The occlusal outline is trapezoidal with the trigonid much narrower than the talonid due to the

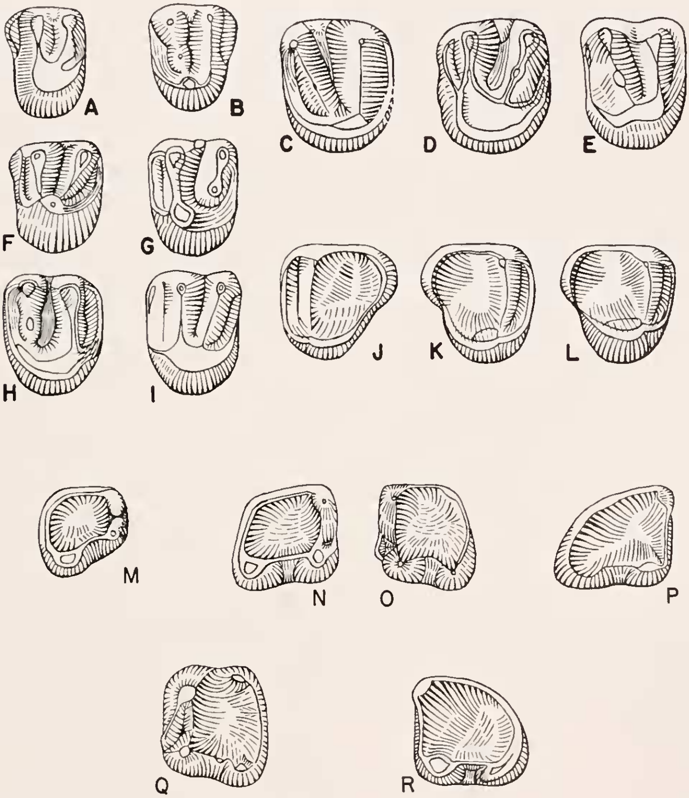

Figure 6. Upper and lower teeth of *Miospermophilus wyomingensis* n. sp., x10. *A,* C.N.H.M. PM2168, LP^4. *B,* A.C. No. 10895, RP^4. *C,* A.C. No. 10896, RM$^{1 \text{ or } 2}$. *D,* C.N.H.M. PM2172, LM$^{1 \text{ or } 2}$. *E,* A.C. No. 10897, RM$^{1 \text{ or } 2}$. *F,* U.W. No. 1409, LP^4. *G,* C.N.H.M. PM2169, LP^4. *H,* C.N.H.M. PM2173, RM$^{1 \text{ or } 2}$. *I,* U.W. No. 1411, LM$^{1 \text{ or } 2}$. *J,* C.N.H.M. PM2174, LM^3. *K,* U.W. No. 1412, RM^3. *L,* U.W. No. 1410, RM^3. *M,* C.N.H.M. PM2213, RP$_4$. *N,* U.W. No. 1414, RM$_{1 \text{ or } 2}$. *O,* U.W. No. 1413, LM$_{1 \text{ or } 2}$. *P,* C.N.H.M. PM2182, RM$_3$. *Q,* Type, A.C. No. 10898, LM$_{1 \text{ or } 2}$. *R,* C.N.H.M. PM2180, LM$_3$. (Anterior end to left except for *B, C, H, K, L, M, N,* and *P.*)

close apposition of the protoconid and metaconid. There is no indication of a complete metalophid and a narrow valley separates the protoconid and metaconid anteriorly. The metaconid is the highest cusp with the protoconid and hypoconid of almost equal height. The entoconid is rather indistinct, being nearly completely incorporated within the posterolophid. There is a short lingual arm from the entoconid to the metaconid. The posterolophid is low and curves gently to the entoconid.

The first and second lower molars are almost identical in structure, with M_1 somewhat squarer in occlusal outline than M_2. The metaconid is the highest cusp with the protoconid and hypoconid much lower and of equal size. The metalophid is generally incomplete, failing to close off the small trigonid basin posteriorly. The anterior cingulum is short and straight, usually without an anteroconid. Mesostylids and mesoconids are variable in their degrees of expression. The entoconid is generally incorporated within the posterolophid, although in some specimens it is present as a distinct cusp. The posterolophid is high and curves sharply at the entoconid angle. The ectolophid is well developed.

M_3 is longer than wide, with the talonid basin greatly enlarged The entoconid is completely incorporated in the swollen posterolophid, which is expanded posteriorly. The anterior cingulum is strong and lacks all trace of an anteroconid. In the absence of a metalophid, the trigonid basin is completely open posteriorly.

Discussion. *Miospermophilus wyomingensis* is closely related to *M. bryanti* and very probably descended from it. Relationships of *M. wyomingensis* to later Miocene spermophiles are uncertain at present, due primarily to the rather poor material known for the rest of the Miocene. The genus *Citellus,* however, probably evolved from *Miospermophilus,* either directly from *M. wyomingensis,* or, more probably from an as yet unknown species of the genus.

Measurements

		N	M
dP^4	a-p	2	1.48
	tr.	2	2.03
P^4	a-p	7	1.55
	tr.	7	2.00
$M^{1 \text{ and } 2}$	a-p	10	1.85
	tr.	10	2.20
M^3	a-p	3	2.04
	tr.	3	2.06

dP_4 a-p	2	1.48
tr.	2	2.04
$M_{1 \text{ and } 2}$ a-p	8	1.88
tr.	8	1.90
M_3 a-p	3	2.10
tr.	3	2.00

CITELLUS Oken

Type species. Mus citellus Linnaeus.

Ground squirrels of the genus *Citellus* are rather common elements of most later Tertiary faunas, particularly throughout the Pliocene of the Great Basin and Mohave-Sonoran areas. However, many of these occurrences are limited to isolated teeth or fragments of mandibles and maxillae with dentitions. Because of the generalized nature of the early ground squirrel dentition, this fragmentary material can tell us very little about the relationships of most of the forms involved, except in a very broad sense, and it is not until the Hemphillian that any definite lineages can be traced leading toward the modern forms. Throughout the Miocene and early Pliocene all ground squirrels are at an otospermophile level of evolution. By the late Pliocene some populations had begun evolving towards the more highly specialized condition seen in the subgenera *Citellus* and *Ictidomys*, but the greatest change in these lines seems to have been a late Pliocene and Pleistocene phenomenon.

Recent ground squirrels can be separated into two groups on dental characters but the recognition of subgenera within these two broad groupings is extremely difficult on this basis alone. The two broad groups are: (1) the more generalized spermophiles of the subgenera *Otospermophilus, Callospermophilus, Poliocitellus,* and *Xerospermophilus*, and (2) the more specialized *Citellus* and *Ictidomys*. In the first, the dentition is low crowned, with low trigonids, low lophs on the upper molars, and long and sometimes complete metalophs on M^{1-2}; in the second, the dentition is high crowned with high trigonids and lophs, and short metalophs on M^{1-2}. The Tertiary ground squirrels all fall into the first category, with the exception of *C. (Citellus) mckayensis* from the Hemphillian of Oregon and a mandible of unknown age (perhaps early Pliocene) from Nebraska. Due to the fragmentary nature of this material and the generalized aspect of the dentitions, I have assigned most of it to the subgenus *Otospermophilus*, the least specialized of Recent ground squirrel subgenera.

Range. Middle Miocene to Recent in North America.

CITELLUS (OTOSPERMOPHILUS) TEPHRUS (Gazin)

Plate 17

Sciurus tephrus Gazin, 1932, p. 59.
Citellus ridgwayi Gazin, 1932, p. 61; Bryant, 1945, p. 354.
Protospermophilus tephrus Bryant, 1945, p. 349.

Type. L.A.C.M. (C.I.T.) No. 332, a partial skull lacking zygomatic arches, posterior part of cranium and left cheek teeth.

Type of synonym. L.A.C.M. (C.I.T.) No. 334, facial region of skull.

Hypodigm. Types and L.A.C.M. (C.I.T.) No. 335, poorly preserved skull lacking basicranium and occiput.

Horizon and locality. Late Hemingfordian, late Middle Miocene. Twenty-eight miles south of Harper and approximately three miles northwest of Skull Spring, Malheur County, Oregon.

Emended diagnosis. Size small; rostrum deep, narrow; zygomatic plate extending only two-thirds of way up rostrum; cheek-pouch muscle pit shallow; infraorbital foramen compressed, slit-like; protocones narrowed; large mesostyles set close to metacones.

In his original description of the sciurids from Skull Springs, Gazin (1932) recognized three forms: *Sciurus malheurensis*, *Sciurus tephrus* and *Citellus ridgwayi*. Bryant (1945) transferred *S. malheurensis* and *S. tephrus* to *Protospermophilus* and left *Citellus ridgwayi* as previously placed by Gazin. It is quite obvious that the skull referred to *Protospermophilus tephrus* represents a true spermophile as do the two skulls assigned to *Citellus ridgwayi*. All three skulls have been distorted considerably through crushing. In the case of the two skulls originally assigned to *Citellus ridgwayi*, this crushing flattened the skulls, particularly in the rostral region, making them appear broad and shallow. In the case of L.A.C.M. (C.I.T.) No. 332 the crushing compressed the skull laterally making it appear much narrower and deeper than it actually was. When these distortions are taken into account, it is clear that only one form is represented. Measurements of the length of the diastema and length of the tooth rows and the patterns of the cheek teeth are essentially identical. Hence, these three skulls are all here referred to *Citellus tephrus*.

Description. The skull is small and rather delicate with a long rostrum which is much deeper than it is broad. The ridges lateral to the incisors are moderately prominent and merge with the dorsal projection of the masseteric fossa. The plate itself is expanded but passes only two-thirds of the way up the side of the rostrum. The infraorbital foramen is compressed into a vertical slit lying immediately above the enlarged masseteric tubercle and only slightly anterior to P^3. The skull is rather broad interorbitally, as is best shown in L.A.C.M. (C.I.T.) No. 335. The palate is broad and the tooth rows nearly parallel.

P^3 is small, simple, and peg-like. The other cheek teeth on the type are rather worn but most of the pattern is discernible. P^4 is much smaller than the other teeth and has a narrow protocone and anterior cingulum. The protoloph on P^4-M^2 is complete and the metaloph only slightly constricted. There is no indication of a protoconule, and the metaconule, while present, is weak on the three teeth. There is a large mesostyle set close to the base of the metacone on M^1 and M^2; on P^4 it is small. The anterior cingula of M^1 and M^2 are not expanded and there is no elevated parastyle. M^3 is as wide as it is long and has neither metaconule nor mesostyle. The posterior cingulum is greatly expanded and is deeply notched at its junction with the protocone.

Discussion. Bryant (1945, pp. 348-349) placed this species in the genus *Protospermophilus* on the basis of its zygomasseteric structure. However, the incomplete development of the zygomatic plate merely represents an evolutionary stage through which most sciurid lines passed at one time or another. The characteristic features of the protospermophiles are not primarily in this structural complex but in the heavier build of the jaws and dentition. *Citellus* (*Otospermophilus*) *tephrus* does not have the heavy lophs and massive cusps of the protospermophiles but is much closer in these characters to the conditions seen in *C. (Otospermophilus) beechyi.* It is smaller than any other Tertiary spermophile, with the exception of *Miospermophilus.*

M. wyomingensis is too advanced to have been ancestral to *C. tephrus.* The lophs of the former species are higher and the metaloph constricted, conditions not seen in *C. tephrus.* However, *M. bryanti* had not acquired these specializations and could have been ancestral to *C. tephrus. C. tephrus* could have given rise to later members of the *Otospermophilus* group although transitional forms are not at present known. It resembles the Barstovian *C. (Otospermophilus) primitivus* in many respects and could have been ancestral to that species.

Measurements

	No. 332	No. 334	No. 335
Length of palate	19.7	21.1	20.5
Alveolar length P^3-M^3	7.8	8.2	8.1

	No. 332		No. 334		No. 335	
	a-p	tr.	a-p	tr.	a-p	tr.
RP^4	1.40	1.90	1.60	2.10	....	....
RM^1	1.80	2.20	1.90	2.40	1.80	2.30
RM^2	1.90	2.30	2.00	2.50	2.00	2.40
RM^3	2.20	2.20	2.20	2.20	2.10	2.20
LP^4	...	....	1.60	2.10	..	....
LM^2	....	....	....	....	2.00	2.50
LM^3	....	....	....	...	2.20	2.20

CITELLUS (OTOSPERMOPHILUS) PRIMITIVUS Bryant

Plate 18, figure 1

Sciurus sp. Douglass, 1903, pp. 153 and 181.

Citellus primitivus Bryant, 1945, p. 352.

Citellus (Otospermophilus) primitivus: Black, 1961a, p. 72.

Type. C.M. No. 746, right mandible with P_4-M_3 lacking angle, condyle, and coronoid.

Hypodigm. Type and C.M. No. 727 a badly crushed and damaged skull and jaws.

Horizon and locality. Upper Barstovian, late Miocene. Type from Madison Valley Formation, Gallatin County, Montana. C. M. No. 727 from 1 mile S. of New Chicago, Granite County, Montana.

Emended diagnosis. Zygomatic plate almost completely sciuromorph; mandible about the size of *Citellus (Otospermophilus) variegatus;* masseteric crest heavy; masseteric fossa deeply concave, pointed anteriorly, ending below anterior roots of M_1; prominent pit posterior to M_3 for medial part of *M. temporalis;* diastemal depression shallow; dentition small in relation to jaw size.

Description. The zygomatic plate is well developed, extending dorsally close to the top of the rostrum, and the maxillary border of the anterior zygomatic root is concave, overhanging the plate area. The cheek-pouch muscle pits are small. There appear to be three transbullar septa. The mandible is slender and the diastema is long with a shallow diastemal depression. The mental foramen is situated slightly below the diastemal surface and midway along its length. The masseteric fossa is deep and limited above and below by heavy ridges. Anteriorly it is pointed, ending below the anterior root of M_1. There is a thin bony ridge continuous with the inner alveolar border which passes backwards to unite with the ascending ramus and which encloses a prominent pit delimiting the area of insertion of the medial part of *M. temporalis.*

P^3 was evidently a small peg, and P^4 is not preserved. M^1-M^2

are low crowned, triangular in outline, with wide anterior cingula, relatively high parastyles and somewhat constricted protocones. The protolophs pass directly across the teeth and the metalophs join the protocone obliquely. Both crests are low and the metaconules small. The metaloph is partially constricted on both M^1-M^2. The mesostyles are large. The posteroexternal portion of M^3 is considerably expanded and there is a faint metaconule present.

P_4-M_3 are low crowned, and M_1-M_2 are rhomboidal in outline with M_2 somewhat more compressed anteroposteriorly than M_1. The protoconid and metaconid of P_4 are so closely appressed that they almost appear to represent one cusp. There is no trace of a trigonid basin on P_4. The posterolophid is low and curves gently through the entoconid corner. There is no distinct entoconid on P_4 and the mesostylid is small. On M_1-M_2 the entoconids are not completely incorporated within the posterolophids. The posterolophids are low and the entoconid corners slightly curved. Distinct mesostylids and mesoconids are present on both teeth. The metalophid on M_1 is weak but does cut off a small trigonid basin while on M_2 the metalophid is not complete and the trigonid basin is open posteriorly. M_3 is similar to M_1-M_2 except that the hypoconid and posterolophid are enlarged.

Discussion. Citellus (O.) primitivus was probably descended from *Citellus (O.) tephrus* of the Hemingfordian. It is more advanced than that species in having large parastyles on M^1-M^2, and a somewhat greater constriction of the metaloph at the protocone. The lophs in both species are very low, however, more so than in the Pliocene otospermophiles, and the metaconcules are small. *Citellus (O.) primitivus* has a more fully developed zygomatic plate and is larger than *C. (O.) tephrus* but these changes are to be expected during the course of ground squirrel evolution and they could have easily evolved from the condition in *C. (O.) tephrus.*

Later species of *Citellus (Otospermophilus)* cannot be traced back to *C. (O.) primitivus* but this is due primarily to the fragmentary nature of so much of the spermophile material. *Citellus (O.) primitivus* was undoubtedly in the main line of spermophile evolution as Bryant (1945) suggested.

Measurements

C.M. No. 746 Type.

Alveolar length P_4-M_3	10.0
Depth below P_4	8.8

	a-p	tr.
I_1	3.70	1.70
P_4	2.00	2.10 —
M_1	2.10	2.30-2.50
M_2	2.30	2.70-2.70
M_3	2.70	2.70-2.20

C.M. No. 727

Alveolar length P^3-M^3	10.0
Alveolar length P_4-M_3	9.8

	a-p	tr.
M^1	2.20	....
M^2	2.30	....
M^3	2.60	2.60
P_4	2.00	1.60-2.00
M_1	2.10	2.30-2.40
M_2	2.40	2.60-2.60
M_3	2.70	2.70-2.20

CITELLUS (OTOSPERMOPHILUS) MATTHEWI[1] n. sp.

Plate 18, figure 2

Sciurus cf. *aberti* Matthew, 1924, p. 84; Bryant, 1945, p. 346.

Type. A.M.N.H. No. 17578, partial right mandible with I, P_4 M_3.

Hypodigm. Type only.

Horizon and locality. Quarry No. 1 Upper Snake Creek Beds. Probably Clarendonian, early Pliocene. Approximately 20 miles S. of Agate, Sioux County, Nebraska. The specimen was collected by an American Museum of Natural History party in 1918. Matthew (1924, p. 63) states, "In 1918 Mr. Thomson's principal collecting was from quarries in *Aphelops* draw." It is quite probable therefore that Quarry No. 1 was located in *Aphelops* draw. A jaw of *Aelurodon haydenianus validus* Matthew and Cook was also obtained from Quarry No. 1 (Matthew, 1924, p. 100). This would appear to date Quarry No. 1 and on this basis I place the age of *Citellus (Otospermophilus) matthewi* as Clarendonian.

Diagnosis. Jaw heavy, deep; masseteric fossa rounded anteriorly below hypoconid of P_4; cheek teeth wider buccally than lingually; high crowned; entoconid corner rounded; posterolophids high; trigonid basins small; no mesoconids or anteroconids; posterior half of M_3 much narrower than anterior half; incisor not greatly compressed.

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[1] Named for the late Dr. W. D. Matthew

Description. The jaw is heavy, more so than in most spermophiles, but in general shape it is very close to that of the Recent *Citellus (Otospermophilus) variegatus.* It is deep below P_4 and also through the posterior portion of the diastema about as in *Sciurus.* The disastema, however, would appear to have been longer in relation to tooth length than in *Sciurus,* and does not drop as abruptly anterior to P_4 as in the tree squirrels. The mental foramen is placed well forward of P_4 and towards the diastemal surface. The masseteric fossa is rounded anteriorly, ending below the posterior half of P_4. It is not deeply concave and its upper border is not well defined.

The cheek teeth increase in size from P_4 to M_3 and, with the exception of P_4, are longer buccally than lingually. There is no indication of an anteroconid on P_4, in which the small trigonid basin opens toward the anterior face of the tooth. The basin is extremely shallow and would be obliterated with little wear, following which the high protoconid and metaconid would appear to be fused into a continuous ridge. The trigonid is much higher than the talonid on P_4. There is no trace of a mesoconid or of a mesostylid. The talonid basin is deep and completely enclosed by the high posterolophid, ectolophid and trigonid. There is no indication of a distinct entoconid and the entoconid corner is rounded. M_1 and M_2 are essentially identical in structure. The trigonid basin is only slightly higher than the talonid basin, with which it is confluent due to the incomplete nature of the metalophid. Anteriorly, the trigonid basin is enclosed by a complete anterior cingulum, which shows no trace of an anteroconid. The buccal valley is deep and becomes broader as it passes internally. The ectolophid and posterolophid are high and the talonid deeply basined. The entoconid corner is rounded with the entoconid submerged in the posterolophid. The mesostylid is also almost completely submerged in the lingual lophid. There is no mesoconid. The protoconid is larger than the hypoconid on both teeth. M_3 is wider than long and much wider anteriorly than across the hypoconid-entoconid. The metalophid is incomplete. The posterolophid and ectolophid are high and the hypoconid and posterior cingulum expanded. The lower incisor is not as greatly compressed as in most sciurids and is moderately convex laterally. The anterior face is rounded, and the enamel extends about halfway down the lateral side of the tooth.

Discussion. Citellus (Otospermophilus) matthewi is typically spermophile-like in its dentition; it is thus rather difficult to understand why Matthew (1924, p. 84) referred it to the living

S. aberti. Bryant (1945, p. 346) followed Matthew in this determination, not having examined the specimen himself. *Citellus (O.) matthewi* has a deeper and heavier jaw than the living spermophiles and the dentition is also heavier and large. Nevertheless, the high posterolophids of M_1-M_2, the complete incorporation of the entoconids in the posterolophids, the rounded entoconid corner, and the shallow diastemal depression clearly indicate ground squirrel affinities. It seems quite obvious that this species was a true spermophile somewhat larger in overall dimensions than the living *Citellus (Otospermophilus) variegatus* but similar to it.

Measurements

Depth below P_4 9.2

Alveolar length P_4-M_3 12.5

	a-p	tr.
I_1	3.40	2.00
P_4	2.60	2.30-2.60
M_1	2.80	3.10-3.10
M_2	3.00	3.40-3.30
M_3	3.50	3.60-3.00

CITELLUS (OTOSPERMOPHILUS) SHOTWELLI[1] n. sp.

Plate 19; Plate 20, figure 1

Citellus sp. Wilson, 1937b, p. 33.

Type. U.O.M.N.H. F-3596 fragmentary skull with RP^3-M^3, LP^4-M^2, right and left mandibles, and partial skeleton.

Hypodigm. Type and U.O.M.N.H. F-7964 left mandible with P_4-M_3, F-7965 left mandible with P_4-M_3, F-7966 right mandible with P_4-M_2, F-7969 left mandible with M_1-M_2, L.A.C.M. (C.I.T.) Nos. 5243 right mandible with M_2-M_3 and 5239 partial left mandible with M_1-M_2.

Horizon and locality. Hemphillian, Pliocene. Type from east bank of McKay Reservoir, 5 miles south of Pendleton, Umatilla County, Oregon. U.O.M.N.H. F-7964, F-7965, F-7966, F-7969 all from the late Hemphillian Westend Blowout local fauna, Oregon; L.A.C.M. (C.I.T.) No. 5243 from the late Hemphillian Arlington beds, Oregon, and L.A.C.M. (C.I.T.) No. 5239 from Hemphillian deposits near Drewsey, Oregon.

Diagnosis. M^1-M^2, M_1-M_2 compressed, much wider than long;

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[1] Named for Dr. J. Arnold Shotwell.

P^4 much smaller than M^{1-3}; paracones and metacones set close together; entoconids distinct on M_1-M_2; posterolophids low, buccal valleys of P_4-M_3 narrow, curving posteriorly; metalophids generally complete on M_2.

Description. The preserved portions of the skull are much too fragmentary to provide any information. The mandible is deep below the alveolar border and is moderately heavy. The diastema is long and the diastemal depression shallow. The masseteric fossa terminates broadly under the hypoconid of P_4. It is deeply concave and the dorsal and ventral borders are heavy. The condyle lies slightly above the alveolar border, and the long axis is directed transversely.

P^3 is a simple, sharply conical peg. The subtriangular P^4-M^2 have narrow protocones and their anterior cingula do not reach the lingual borders. The anterior cingulum on P^4 is narrow and there is no indication of a parastyle, whereas on M^1-M^2 the cingulum is wider and the parastyle is prominent. The lophs are high, the metaconules large, and the metalophs incomplete, except at extreme stages of wear on P^4-M^2. Mesostyles are very small and set at the base of the paracone slopes. The paracones and metacones are close together with only a narrow valley between them. The posterior cingula are narrow and not greatly expanded toward the protocones. On M^3, the posterior cingulum bends sharply posteriorly from the protocone and the posteroexternal portion of M^3 is expanded. The parastyle is not as well developed on M^3 as it is on M^1-M^2.

P_4 is trapezoidal, M_1-M_3 rhomboidal, and M_{1}-$_{2}$ much wider than long. The protoconid and metaconid of P_4 are closely appressed with only a shallow notch separating them that is quickly obliterated by wear. There is neither anteroconid, nor mesostylid nor mesoconid on P_4. The posterolophid is low and passes straight across P_4 to the lingual margin, where it curves anteriorly to end at the small entoconid. The ectolophid is low and the buccal valley deep and narrow. The trigonid on M_1-M_3 is only slightly higher than the talonid. The metalophid is short and lies progressively farther down the metaconid slope from M_1 to M_3. In the Arlington specimen, L.A.C.M. (C.I.T.) No. 5243, the trigonid of M_{2}-$_{3}$ is higher than in the type and Westend Blowout material, and the metalophid on M_2 is complete. The posterolophid is low and terminates in a small but distinct entoconid. The buccal valley is narrow and deep and swings posteriorly as it passes internally. Small mesostylids are present on M_1-M_3. In L.A.C.M. (C.I.T.) No. 5239 the entoconid of M_{1}-$_{2}$ is not as distinct and the posterolophid is rather blade-like at the entoconid corner. The incisor has a rounded lateral face and is only moderately compressed.

The skeletal elements preserved include right and left radius and ulna, distal end of the left tibia, right calcaneum, and part of the right hind foot. The radius and ulna are longer and considerably broader distally than those of *C. (Otospermophilus) variegatus.* This is particularly true for the distal end of the radius. The distal end of the tibia, however, agrees almost perfectly in size with that of the living species. The calcaneum is rather more heavily built and the metatarsals somewhat longer than in the Recent forms.

Discussion. All of the material here referred to *C. (Otospermophilus) shotwelli* differs from *C. (O.) wilsoni* in having M^1-M^2 and M_1-M_2 wider than long, and from *C. (O.) gidleyi* in larger size. The specimens from McKay Reservoir, Westend Blowout, Drewsey, and the Arlington beds resemble each other more closely than they do any other Pliocene population of spermophile and the differences between the samples from these localities are primarily those of size. Among contemporaneous forms *C. (O.) shotwelli* is closest to *C. (O.) gidleyi* and these two species quite probably had a common ancestry in the early Pliocene. *C. (Otospermophilus) shotwelli,* particularly the Westend sample, is closer to the Recent *C. (Otospermophilus) beechyi* than to any other Recent otospermophile and would appear to be in the phyletic line leading to the Recent species.

Measurements

	F-3596	F-7964	F-7965	F-7966
Length of mandible	41.0	....	....	....
Length of diastema	9.5	....	....	....
Depth of mandible below P_4	8.5	8.3		7.5
Alveolar length P_4-M_3	11.1	10.8	10.6	11.0

	F-3596	
	a-p	tr.
P^4	2.30	2.80
	2.30	2.80

M^1	2.60	3.30
	2.60	3.30
M^2	2.60	3.20
	2.60	3.30
M^3	3.20	3.20

	F-3596	F-7964	F-7965	F-7966
I_1 a-p	2.90			
tr.	1.60			
P_4 a-p	2.30	2.40	2.20	2.30
tr.	2.00-2.60	2.00-2.50	1.90-2.40	2.00-2.50
M_1 a-p	2.40	2.40	2.30	2.50
tr.	3.00-3.20	2.60-2.80	2.80-2.90	3.00-3.00
M_2 a-p	2.60	2.50	2.50	2.70
tr.	3.30-3.30	3.00-3.10	3.20-3.20	3.30-3.20
M_3 a-p	3.20	3.20	3.10	
tr.	3.40-3.00	3.20-2.90	3.20-2.90	

	F-7969	L.A.C.M. (C.I.T.) 5239	L.A.C.M. (C.I.T.) 5243
M_1 a-p	2.40	2.50	
tr.	2.90-3.00	2.90-3.10	
M_2 a-p	2.60	2.70	2.70
tr.	3.20-3.20	3.30-3.30	3.50-3.50
M_3 a-p			3.50
tr.			3.70-3.00

CITELLUS (OTOSPERMOPHILUS) GIDLEYI
(Merriam, Stock and Moody)
Plate 20, figure 2

Otospermophilus gidleyi Merriam, Stock and Moody, 1925, p. 68.
Citellus (Otospermophilus) gidleyi: Bryant, 1945, p. 353.

Type. U.C.M.P. No. 26793, incomplete horizontal ramus of left mandible with P_4-M_3.

Hypodigm. Type only.

Horizon and locality. Hemphillian, Middle Pliocene. About 5½ miles west of Dayville, Grant County, Oregon.

Emended diagnosis. Smaller than Recent species of *Citellus (Otospermophilus)*; posterolophid low; lingual notch shallow; trigonid basins enclosed posteriorly by complete metalophid; mesostylid present on M_1-M_2; small ectostylids on M_1-M_3.

Description. The mandibular ramus is deep in relation to overall size, and the diastemal depression is shallow. The masseteric fossa is rounded anteriorly and more deeply concave than in Recent species. The protoconid and metaconid are closely appressed on P_4, the anterior half of the tooth being thus much narrower than the posterior. The posterolophid is low and there is no mesostylid or ectostylid. M_1 and M_2 are compressed anteroposteriorly. The posterolophids curve gently to the entoconid corner and terminate in small but distinct entoconids. The mesostylids are set off from both the entoconids and metaconids by shallow notches. The buccal valleys constrict internally. The protoconids and hypoconids are of equal size. The metalophids are complete and the trigonid basins are enclosed as small pits. The hypoconid and posterolophid of M_3 are moderately expanded and there is no mesostylid; in all other respects this tooth resembles M_1 and M_2.

Discussion. As has been pointed out (see p. 204), *C. (Otospermophilus) gidleyi* resembles *C. (Otospermophilus) shotwelli* in almost all respects. It is a decidedly smaller species, however. The similarity of the two would suggest a common ancestry probably in the late Clarendonian. No descendants of *C. (O.) gidleyi* are known.

Measurements

Depth of mandible below P_4		8.6
Alveolar length P_4-M_3		8.4
	a-p	tr.
I_1	1.50	2.80
P_4	1.80	1.40-2.20
M_1	1.80	2.20-2.20
M_2	2.00	2.50-2.50
M_3	2.50	2.50-2.20

CITELLUS (OTOSPERMOPHILUS) ARGONAUTUS Stirton and Goeriz

Otospermophilus argonautus Stirton and Goeriz, 1942, p. 462.
Citellus sp. Kellogg, 1910, p. 427; Bryant, 1945, p. 356.
Citellus? species Wilson, 1936, p. 19; Bryant, 1945, p. 358.
Citellus sp. Wilson, 1937a, p. 14; Bryant, 1945, p. 356.

Type. U.C.M.P. No. 34281, part of right lower jaw with P_4 and partial M_1.

Hypodigm. Type and U.C.M.P. No. 34280, left ramus without dentition, L.A.C.M. (C.I.T.) Nos. 1794 a partial left ramus with M_2, 1795 a right ramus without dentition, 1965 a partial right ramus with P_4-M_2, 5240 RI^1 and LI_1, 5241 a partial right ramus without dentition and U.C.M.P. No. 12570 a worn RM_1.

Horizon and locality. Hemphillian, Middle Pliocene. Type from Charles E. Schell ranch, site 1 in andesitic tuff, 5 miles west of Knights Ferry, Stanislaus County, California, U.C. Loc. V. 3813. L.A.C.M. (C.I.T.) Nos. 1794 and 1795 from Smiths Valley local fauna, Lyon County, Nevada; L.A.C.M. (C.I.T.) Nos. 1965, 5240, and 5241 from Kern River local fauna, Kern County, California; and U.C.M.P. No. 12570 from Thousand Creek local fauna, Humboldt County, Nevada.

Emended diagnosis. Smaller than *Citellus (Otospermophilus) shotwelli* and *wilsoni,* near size of *C. (O.) gidleyi;* M_1-M_2 not as greatly compressed anteroposteriorly as in *C. (O.) gidleyi;* ectolophids heavy, set well in from buccal margin; mandible heavier than in *C. (O.) gidleyi.*

Description. The diastemal depression is shallow, and the diastema only moderately long. The main area of the masseteric fossa terminates under the anterior end of M_1, but a broad scar extends forward beyond it to a point under P_4.

The protoconid and metaconid of P_4 are closely appressed with a shallow groove between them on the anterior face. The buccal valley is deep and narrow. The ectolophid is strong with no indication of a mesoconid. The posterolophid curves through the entoconid corner with no indication of a distinct entoconid. There is no mesostylid. On M_1-M_2 the anterior cingulum and metalophid are strong and enclose a small trigonid basin. The ectolophid is prominently developed and the buccal valley narrow and deep.

Discussion. Although represented in four different faunas in California and Nevada, *Citellus (O.) argonautus* is still known from only the most fragmentary material. However, the low-crowned cheek teeth and low trigonids clearly indicate that this species is an otospermophile. It is a smaller species than *C. (O.) shotwelli* and *wilsoni. C. (O.) argonautus* differs from *C. (O.) gidleyi* in the greater suppression of the entoconid within the posterolophid and the squarer outline of M_1-M_2. *C. (O.) argonautus* may have been ancestral to *C. (O.) bensoni* of the early Pleistocene but the material available is inadequate to be certain of this relationship.

Measurements

Type U.C.M.P. No. 34281

	a-p	tr.
P_4	2.10	1.80-2.20
M_1	....	2.40- ...

L.A.C.M. (C.I.T.) No. 1965

Alveolar length P_4-M_3	8.8
Depth of mandible below P_4	5.6

	a-p	tr.
P_4	1.70	1.40-1.90
M_1	1.70	....- ....
M_2	2.10	....-2.40

L.A.C.M. (C.I.T.) No. 1794

	a-p	tr.
M_2	2.10	...-2.50

U.C.M.P. No. 12570

	a-p	tr.
M_1	2.10	2.00-2.20

CITELLUS (OTOSPERMOPHILUS) WILSONI Shotwell

Plate 21

Citellus (Otospermophilus) wilsoni Shotwell, 1956, p. 728.

Type. U.O.M.N.H. F-4097, right mandible lacking incisor, condyle, coronoid, and anterior tip of jaw.

Hypodigm. Type and U.C.M.P. No. 55611, a nearly complete skull, U.O.M.N.H. F-3634 left maxillary fragment with M^1, F-3635 left maxilla with P^4-M^3, F-3636 right maxillary fragment with P^4-M^1, F-3612 fragment of right mandible, F-3628 fragment of right mandible with P_4-M_1, F-3629 fragment of right mandible with M_1-M_2, F-3494 fragment of right mandible, F-2658 fragment of left mandible, F-4085 fragment of left mandible with P_4 and M_2, F-4098 fragment of left mandible, L.A.C.M. (C.I.T.) Nos. 5246, a partial skull, 5244 a right mandible with P_4-M_3 and 5245 an edentulous left mandible and several isolated teeth and foot bones.

Horizon and locality. U.C.M.P. No. 55611 Clarendonian; Ellensburg, Washington. Type and U.O.M.N.H. F-3634, F-3635, F-3636, F-3612, F-3628, F-3629, F-3494, F-2658, F-4085, F-4098 Hemphillian; east bank of McKay Reservoir, 5 miles south of Pendleton, Umatilla County, Oregon. L.A.C.M. (C.I.T.) Nos. 5244-5246 (data from Dr. T. Downs), Hemphillian; Loc. 375 near common corner of Sections 29, 30, 31, and 32, T.3N., R.22E., about 5 miles SE, of Arlington, Gilliam County, Oregon.

Emended diagnosis. Near size of *Citellus (O.) shotwelli;* molars rhomboidal in outline, not as greatly compressed anteroposteriorly as in *C. (O.) shotwelli;* metaloph incomplete, metaconule large on P^4-M^2; entoconid completely incorporated within posterolophid; metalophid progressively shorter from M_1-M_3, leaving trigonid basin open into talonid basin on M_2-M_3; ectolophids high, set well in from buccal margins on P_4-M_3.

Description. The skull resembles that of *C. (O.) variegatus* in most respects. The infraorbital foramen is nearly triangular, compressed dorsally and broad ventrally. The masseteric tubercle is large and lies at the ventrolateral corner of the infraorbital foramen. The zygomatic plate and masseteric fossa are completely sciuromorph and the notch in the zygomatic plate is opposite the middle of M^1. The mandible is moderately heavy and deep, the diastemal depression shallow, and the masseteric fossa ends broadly below the hypoconid of P_4.

P^4-M^2 are subtriangular in outline with narrow protocones but with broad posterior cingulum-protocone connections. The anterior cingulum is low and short, merging into the protocone well down on the anterior face on P^4. On M^1-M^2 the anterior cingula are broader, bear large parastyles, and do not pass to the lingual borders. The posterior cingulum rises to the top of the protocone on P^4-M^2. On all three teeth the lophs are low, the metaconules large and the metalophs incomplete. The paracones and metacones are widely separated. Small mesostyles are present on P^4-M^2. There is a small metaconule on M^3, which is joined to the base of the protocone by a low loph. The posteroexternal portion of M^3 is expanded and there is a shallow notch between it and the posterior slope of the protocone.

P_4 is trapezoidal in outline. A deep notch, partially blocked anteriorly by a small anteroconid, divides the protoconid and metaconid for about one-third of the distance down the crown. The ectolophid is high and narrow, the buccal valley is broad, and the posterolophid is constricted at the hypoconid and terminates internally at the entoconid, leaving a notch between the entoconid and metaconid. M_1-M_2 are not greatly compressed anteroposteriorly but the degree of anteroposterior compression of M_3, which is no longer than wide, is especially notable. The position of the metalophid shifts from M_1 to M_3. On M_1 it is complete and closes off the small trigonid basin, on M_2 it passes to the base of the metaconid slope, and on M_3 it passes into the talonid basin. The posterolophids are high and pass through the entoconid areas to small mesostylids. The ectolophids on M_1-M_3 are high, narrow ridges set well in from the buccal margins, and the buccal valleys are broad and deep.

Discussion. Citellus (Otospermophilus) wilsoni differs markedly from *C. (O.) shotwelli* and *C. (O.) gidleyi* in possessing upper and lower molars which show very little anteroposterior compression. In this respect *C. (O.) wilsoni* agrees with the Recent *C. (O.) variegatus* and differs from *C. (O.) beechyi.* The Clarendonian skull, here referred to *C. (O.) wilsoni,* also shows a close resemblance to *C. (O.) variegatus* as well as to other Recent species of the subgenus. By the early Pliocene most features of the skull and dentition, characteristic of modern species of *Otospermophilus,* have appeared and two distinct phyletic lines, culminating in two living species, can be recognized. The changes which took place between the early Pliocene and the present in the *C. (O.) wilsoni* to *C. (O.) variegatus* line are, as far as can be told from the material available, extremely small and consist of a slight increase in size, a slight elevation of the protoloph and metaloph, expansion of the anterior cingulum on M^1-M^2, loss of the mesostyle, and slight elevation of the ectolophid and posterolophid on M_1-M_2. All these changes are ones of degree and, as stated above, are rather trivial. However, taken together and considerng the age of the material, I believe these Pliocene forms should be considered as distinct from the Recent species.

Measurements

U.C.M.P. No. 55611

Length of skull			50.8
Width of rostrum at anterior end of zygomatic plate			11.5
Depth of rostrum at anterior end of zygomatic plate			9.8
Width of skull at supraorbital notch			12.9
Width of skull at postorbital notch			14.3
Length of diastema			13.3
Alveolar length P^3-M^3			10.2
		a-p	tr.
	I^1	3.35	1.70
		3.35	1.70
	P^4	2.00	2.50
		2.00	2.50

M^1	2.40	2.80
	2.30	2.90
M^2	2.40	3.10
	2.40	3.10
M^3	2.70	2.90
	2.70	2.90

U.O.M.N.H. Nos.	F-4097	F-4085
Length of diastema	—	8.5
Depth of mandible below P_4	8.3	7.8
Alveolar length P_4-M_3	11.2	approx. 11.5
P_4 a-p	2.30	2.30
tr.	1.90-2.50	1.90-2.40
M_1 a-p	2.40	
tr.	2.60-2.90	
M_2 a-p	2.70	2.80
tr.	3.00-3.00	3.20-3.20
M_3 a-p	3.20	
tr.	3.20-2.80	

U.O.M.N.H. No. F-3635		
Alveolar length P^3-M^3		11.8
	a-p	tr.
P^4	2.40	2.50
M^1	2.50	3.10
M^2	2.70	3.20
M^3	3.10	3.10

L.A.C.M. (C.I.T.) No. 5246		
Width of skull at supraorbital notch		12.5
Width of skull at postorbital notch		16.3
Alveolar length P^3-M^3		11.3
	a-p	tr.
I^1	3.20	1.70
P^3	1.20	1.40
P^4	2.20	2.80
M^1	2.50	3.40
M^2	2.60	3.50
M^3	2.60	3.10

L.A.C.M. (C.I.T.) Nos.	5244	5245
Length of mandible approx.	36.0	—
Length of diastema	9.5	9.5
Depth of mandible at mental foramen	6.0	—

CITELLUS (OTOSPERMOPHILUS) FRICKI Hibbard
Plate 22, figure 1

Citellus (Pliocitellus) fricki Hibbard, 1942, p. 253, 2 pls.

Type. F:A.M. No. 24627, skull with I, P^3-M^3, lacking squamosal, jugal and bullae; left ramus, lacking angle and M_3; right humerus, radius and ulna, left humerus, radius and ulna, some carpals, left tibia, partial right tibia; various vertebrae.

Hypodigm. Type only.

Horizon and locality. Ogallala Formation, Hemphillian, Pliocene. J. Swayze Quarry, Clark County, Kansas.

Emended diagnosis. Near *C. (Otospermophilus) variegatus* in size; cranium not as inflated as this species; pits for dorsal cheek pouch muscles only slightly developed; P^3 peg-like with no trace of an anterior and lingual cingulum; M^3 short; M_1-M_2 extremely compressed on lingual side.

Hibbard (1942, p. 253) stated that the characters of the subgenus *Pliocitellus* were those of the type species *Citellus fricki.* However, all characters of the species are those of the subgenus *Otospermophilus* with the exception of the extremely simple P^3 and the great buccal compression of M_2. In my opinion these two characters do not warrant subgeneric distinction and *Citellus fricki* is here placed in the subgenus *Otospermophilus.*

Description. The skull resembles that of *C. (Otospermophilus) variegatus* in most respects. The dorsal profile is rounded; the rostrum is relatively long and slender; the cranium is moderately inflated, although not as much so as in the Recent species. The zygomatic plate is fully developed, rising to the dorsal surface of the rostrum. The maxillary root of the zygomatic arch is not as deeply concave as in the Recent species, however. The zygomatic plate is not as steeply inclined, and the zygomatic notch is opposite P^4-M^1 rather than opposite the posterior half of M^1 as in *C. (Otospermophilus) variegatus.* The infraorbital foramen is vertically compressed and slit-like and the masseteric tubercle is large. The cheek-pouch muscle pits are small. The palate is narrow and the alveolar borders are set considerably below it. The paroccipital processes are short and flattened.

The mandibular ramus is slightly smaller than that of *C. (Otospermophilus) variegatus*, but agrees with it in all other respects. The diastema is long and the diastemal depression shallow. The mental foramen lies about halfway between P_4 and the incisor, just below the superior border of the mandible. The masseteric fossa is somewhat constricted anteriorly and ends below the posterior half of P_4. The condyle lies slightly above the alveolar border, as in *C. (Otospermophilus) variegatus,* but differs from that species in having the long axis of the condylar face directed anteroposteriorly rather than transversely.

P^3 resembles that of *Sciurus* more closely than that of *Citellus.* It is a simple peg with no cingulum around the base of the principal cusp, and is smaller than in Recent spermophiles. P^4-M^3 are mesodont and although well worn are clearly very similar to those of *C. (Otospermophilus) variegatus.* P^4-M^2 are roughly triangular, with low lophs, broad anterior cingula, low parastyles, and short, narrow posterior cingula. The metalophs are partially constricted, and metaconules are present. There are no mesostyles. M^3 is broadly triangular with only a slight expansion of the posteroexternal corner. A large mesostyle is present at the base of the paracone. The enamel of the compressed upper incisors is smooth.

Much of the pattern of P_4-M_2 has been obliterated by wear but these teeth nevertheless appear to have been typically otospermophile-like, with the exception of a greater anteroposterior compression of M_1-M_2, and an extreme shortening of lingual length in relation to buccal length. There is no anteroconid on P_4, and the protoconid and metaconid are closely appressed with only a shallow furrow separating them anteriorly. The entoconid corner is angular and the posterolophid low. The buccal valley is shallow on this tooth and on M_1 and M_2. M_1 and M_2 agree in pattern, but M_2 is more compressed lingually. The posterolophids on both pass anterobuccally to the entoconids, which are placed forward near the base of the metaconids. No mesostylids are present.

The limb bones are all somewhat smaller than those of *C. (Otospermophilus) variegatus* but compare with them in most respects. The humeri appear to be identical. The lateral fossa of the ulna is not as deeply excavated as in the Recent species, but the ulna and the radius of *C. fricki* agree in all other respects. The lateral and caudal fossae of the tibia are deeper in *C. fricki,* with the cranial, medial, and interosseous borders sharper and more distinctly elevated than in *C. (O.) variegatus.* In all other characters they agree. Both the scapula and pelvis are too poorly preserved for comparison with the Recent species. The calcaneum and metatarsals agree with those of *C. (O.) variegatus.*

Discussion. Citellus (Otospermophilus) fricki differs markedly from *C. (O.) tephrus* of the Middle Miocene and *Citellus (O.) primitivus* of the Flint Creek in the following characters: (1) a more elongate skull; (2) complete attainment of sciuromorph zygomasseteric structure; (3) somewhat higher crowned cheek teeth; (4) greater anteroposterior compression of P^4-M^2 and M_1-M_2. It is also, of course, much larger than *C. tephrus,* and somewhat larger and of different proportions than the Flint Creek spermophile. The skull of *C. (O.) fricki* differs considerably from *C. matachicensis* in general proportions, being much more elongate and probably not as wide across the zygomatic arches as that species. The cheek teeth in the two also differ on several counts.

The skull of *C. fricki* agrees rather well with that of the Recent *C. (Otospermophilus) variegatus* but is not as advanced as regards the degree of inflation of the cranium, the angle of the zygomatic plate, and the position of the articular surface of the condyle. It is highly specialized in the extreme compression of M_1-M_2 and in the absence of cingula on P^3 and these characters would seem to remove it from the ancestry of the later otospermophiles. On the basis of the compression of M_1-M_2 it may be related to the earlier, Clarendonian, *C. (Otospermophilus)* sp. from the Ingram Creek sites of California.

Measurements

Length of skull	57.2
Width of skull at supraorbital notch	15.5
Width of skull at postorbital notch	16.0
Width across occiput	22.5
Width of rostrum at anterior end of zygomatic plate	11.0
Depth of rostrum at anterior end of zygomatic plate	11.3
Length of diastema I^1-P^3	15.5
Palatal width at M^1	7.5
Alveolar length P^3-M^3	10.5
Length of mandible	39.5
Length of diastema	8.5
Depth below M_1	7.8
Alveolar length P_4-M_3	10.2

	a-p	tr.
I	3.90	1.95
P^3	1.20	1.20
P^4	2.00	2.70
M^1	2.50	3.20
M^2	2.60	3.30
M^3	2.70	3.10
I	3.10	1.75

P_4	2.00	1.75-2.30
M_1	2.20	2.70-2.90
M_2	2.50	3.20-3.10
Length of humerus		37.5
Length of ulna		39.3
Length of radius		31.5
Length of tibia		49.5
Length of calcaneum		11.5

CITELLUS (OTOSPERMOPHILUS) PATTERSONI Wilson

Plate 22, figure 2

Citellus pattersoni Wilson, 1949c, p. 170.

Type. L.A.C.M. (C.I.T.) No. 3547, right P^4-M^3.

Hypodigm. Type only.

Horizon and locality. Hemphillian, Pliocene. Yepomera local fauna. California Institute of Technology Vertebrate Paleontology Loc. 296, Arroyo de Los Jises, Matachic, Chihuahua, Mexico.

Diagnosis. Largest known species of genus; metaloph strong on M^3.

Description. The teeth are greatly enlarged and high crowned, but agree in most other respects with those of *C. (Otospermophilus) variegatus;* the only major difference in pattern is the presence of a strong metaloph on M^3 of *C. (O.) pattersoni.* P^4-M^2 are subtriangular in outline with high protocones. The anterior cingulum on P^4 is very low, joining the protocone well down near the base of the cusp. On M^1-M^2 it is low for most of its course but rises to join the protocone about two-thirds of the way up the slope. Parastyles are well developed on all teeth. The protolophs and metalophs are very high on P^4-M^3 and pass directly across the teeth, while the metalophs pass obliquely linguad from the metacones. The metalophs are constricted and large metaconules are present. The posterior cingulum on P^4-M^2 rises to the top of the protocone. Extremely small mesostyles are present. The posteroexternal corner of M^3 is expanded; the metaloph, although strong, is much lower than the protoloph and passes to the base of the protocone.

Discussion. C. (Otospermophilus) pattersoni is easily distinguished from other Tertiary sciurids by its large size combined with a rather primitive otospermophile dentition. As Wilson (1949c) has pointed out, this species resembles *Marmota* only in its large size; the teeth are higher crowned, the protocones are broader, and the metaloph is more constricted at the protocone than in that genus. *C. pattersoni* is smaller than *Paenemarmota.* Also P^4 is smaller than M^1 in *C. pattersoni* while the reverse is true for *Paenemarmota.* There is no special resemblance between *C. pattersoni* and either *Arctomyoides* or *Palaearctomys.* The affinities of *C. pattersoni* seem to be closest to the *Otospermophilus* group of ground squirrels from which it differs only in size and in the presence of a strong metaloph on M^3.

Measurements

	a-p	tr.
P^4	4.10	5.40
M^1	4.30	6.10
M^2	4.50	6.30
M^3	5.10	5.80

CITELLUS (OTOSPERMOPHILUS) sp.

Referred Specimens. U.C.M.P. Nos. 35925, partial left mandible without cheek teeth, 35926, partial left mandible with P_4-M_1, 35928, partial right mandible with P_4-M_1, 35930, incomplete right maxilla with P^4-M^3, 35953, LM^1.

Horizon and locality. Clarendonian, early Pliocene. Ingram Creek Site 2, Loc. V-3952 Stanislaus County, California, and U.C.M.P. No. 35953 Ingram Creek Site 1B, Loc. V-3951.

Description. The maxillary fragment reveals that the major portion of the large masseteric tubercle lies ventral to the infraorbital foramen, which is not greatly compressed, and that the zygomatic notch is opposite the middle of M^1. The mandible is somewhat more lightly built and not as deep as that of the Recent otospermophiles. The diastemal depression is shallow and the diastema long. The major portion of the masseteric fossa ends below the anterior end of M_1, but a large crescentic scar extends forward and dorsal to the main fossa.

P^3 is missing but its presence is indicated by a large alveolus. P^4-M^2 are essentially identical in structure. The protocone is large but the lingual margins of the teeth are narrower than the buccal margins. The anterior and posterior cingula are short and join the protocone in smooth curves on M^1 and M^2. On P^4 the anterior cingulum is low and passes into the base of the protocone. The metaloph is incomplete and a large metaconule is present. The mesostyle is small on M^1-M^2 and lacking on P^4. M^3 is slightly wider than it is long with little expansion of the posterior cingulum; there is no indication of a metaconule and only a small mesostyle.

Only P_4 and M_1 are preserved and in both known specimens they are deeply worn. There is a slight indication of an anteroconid on P_4 of U.C.M.P. No. 35928 but none on U.C.M.P. No. 35926. The protoconid and metaconid are closely appressed, with no trigonid basin intervening and the entoconid angle is rounded. There is no indication of a mesoconid or mesostylid. All detail of crown pattern has been eliminated on M_1. The tooth is quadrate, rather sharply angled at the entoconid corner and much wider than long. The lower incisor is compressed; the anterior and lateral faces are rounded and the enamel extends nearly halfway down the lateral side.

Discussion. This form appears to be a typical, generalized ground squirrel. It is much closer structurally to the *Otospermophilus-Callospermophilus* group of ground squirrels than to other subgenera of the genus but it is impossible to assign it to one or the other of these subgenera on the material available. There is a suggestion of possible relationship to *C. (Otospermophilus) fricki,* especially in the lingual compression of M_1, but in the absence of M_2 in any of this material this relationship cannot be substantiated.

Measurements

		a-p	tr.
U.C.M.P. No. 35930			
	P^4	2.20	2.80
	M^1	2.40	3.00
	M^2	2.40	3.10
	M^3	2.70	2.80
U.C.M.P. No. 35926			
	I	3.10	1.60
	P_4	2.20	2.00-2.50
	M_1	2.50	2.80-3.00
U.C.M.P. No. 35928			
	P_4	2.30	2.00-2.50
	M_1	2.50	2.80- —

CITELLUS MATACHICENSIS Wilson

Plate 22, figure 3

Citellus matachicensis Wilson, 1949, p. 171.

Type. L.A.C.M. (C.I.T.) No. 3551, nearly complete skull, mandible, ulna, radius, pelvis, sacrum, tibia and various foot bones.

Hypodigm. Type only.

Horizon and locality. Hemphillian, middle Pliocene, Yepomera local fauna. California Institute of Technology Vertebrate Paleontology Loc. 299. Matachic, Arroyo de los Pinos, Chihuahua, Mexico.

Emended diagnosis. Rostrum short, of nearly uniform width; zygomatic breadth relatively great; ectopterygoid plates well developed; mesostyles minute; cheek teeth high crowned but lophs and posterolophids low; metaconule on M^3 small; posterlophids low.

Description. The skull resembles that of *C. (Callospermophilus) lateralis* in general proportions, although it is somewhat larger. The rostrum is short and does not taper anteriorly. The interorbital width is greater than that of *C. (Otospermophilus)* and about as in *C. (Callospermophilus)*. The supraorbital notches are large and open laterally, and the postorbital bars are long and slender. The cranium is broad across the posterior zygomatic roots and narrows considerably at the postorbital bars, thus appearing rather globular in outline. The lambdoidal crests are prominent, but this has been accentuated by a slight crushing of the cranium, which has been pushed under the dorsal margin of the occiput.

The nasals extend back beyond the premaxillary-frontal suture, meeting the frontals at the level of the anterior ends of the orbits. The premaxillary-maxillary suture passes anteriorly along the dorsal surface of the skull and then drops straight down at the anterior edge of the zygomatic plate to the ventral surface of the rostrum, where it bends forward to the incisive foramen. The zygomatic plate is fully developed, reaching the dorsal surface of the rostrum where it ends in a distinct pit just behind the premaxillary-maxillary suture. The plate is deeply concave and overhung by an extensive projection of the maxillary root of the zygoma. The infraorbital foramen lies just above and anterior to P^3, and is oval. The masseteric tubercle is large and situated at the lateroventral margin of the foramen. The zygomatic notch lies opposite the posterior end of M^1.

The palate is short and broad, with the tooth rows converging posteriorly. Just behind the incisors there are moderately developed cheek-pouch muscle pits. Opposite M^2 the maxillary-palatine suture passes in a straight line to the middle of the palatine foramina, where it bends posteriorly. The pterygoid fossae are broad, with the pterygoid plates converging posteriorly and the ectopterygoid plates flaring laterally. The buccinator and masticatory foramina are separate.

The posterior zygomatic root extends well out from the cranium, giving the skull a wide zygomatic breadth. The jugal extends to the anterior tip of the orbit behind the maxilla. It is expanded and faces ventrolaterally throughout most of its length. The squamosal extends up the lateral wall of the cranium to a point just below the postorbital bar. The bullae are nearly circular, with their widths almost equaling their lengths. The foramen magnum is elliptical and much wider than in *C. (Callospermophilus) lateralis*. The occiput is also broader in relation to its height than in that species.

The mandible is rather heavy and the diastema short relative to the alveolar length. The diastemal depression is extremely shallow and the mental foramen lies just below the dorsal surface and closer to the incisor than to P_4. The masseteric fossa ends broadly under the posterior end of P_4. The long axis of the condyle is directed transversely rather than anteroposteriorly as in Recent species.

P^3 is small and rises to a steep peak that is supplemented only by a very narrow internal cingulum. P^4-M^3 are high crowned, particularly internally, more so than in Recent species of *Otospermophilus* or *Callospermophilus*, although in pattern they resemble the cheek teeth of these subgenera more closely than they do those of the more specialized ground squirrels of the subgenera *Citellus* and *Ictidomys*. The anterior cingula on P^4-M^2 are short and are set off from the protocones, lying well below the tops of the lophs. The protolophs are moderately high, but lie below the apices of the protocones. The metalophs are set off from the protocones, ending in large metaconules. The posterior cingula rise gently to the apices of the protocones. Small mesostyles are present on all cheek teeth. M^3 is not greatly expanded posteriorly. There is a small metaconule part way down on the buccal slope of the protocone. The anterior cingulum is somewhat larger than on P^4-M^2 and rises to the apex of the protocone. The upper incisors are not as recurved as in Recent species, and their tips are perpendicular to the occlusal surface of the cheek teeth.

The lower molars are high crowned but in pattern are closer to those of the lower crowned *Callospermophilus* than to those of any other group of ground squirrels. The buccal valley on P_4 is broad and shallow and the protoconid and metaconid closely appressed. The posterolophid is low and curves to a small but distinct entoconid. There is no mesoconid or mesostylid on any cheek tooth. M_1-M_2 are rhomboidal, with moderately elevated trigonids and low posterolophids. The entoconid corners are curved and there is a distinct notch between the end of the posterolophid and the base of the metaconid. The trigonid basins are small and completely enclosed by the metalophids. The buccal valleys are constricted and deep. On M_3, the metalophid is weak, joining the metaconid much farther down its posterior slope than is the case on M_1 or M_2. The posterolophid is enlarged and heavy.

The skeletal elements of *C. matachicensis* are similar to those of *C. (Otospermophilus) variegatus* differing primarily in their smaller size and more slender proportions. The lateral fossa of the ulna is not as deeply concave as that of the Recent species and the distal half of the radius is broader in *C. matachicensis*. The proximal third of the right femur and the distal two-thirds of the left tibia also agree with those of *C. (Otospermophilus) variegatus*. The presence of four sacral vertebrae has been mentioned by Wilson. Bryant (1945) found that over 50 per cent of all ground squirrels have four sacrals, but that only in the subgenus *Ictidomys* were four sacrals present in all specimens examined. He points out that the higher number of sacral vertebrae is correlated with increased fossorial specialization. The presence of four sacrals in *C. matachicensis* would indicate that selection for improved fossorial habit had begun at least by the Hemphillian and probably earlier.

Discussion. Citellus matachicensis combines characters which are found in several of the Recent subgenera of *Citellus*. For this reason Wilson (1949c) did not refer it to any of the Recent subgenera and I have followed him in this. The skull resembles that of *Callospermophilus* and to a less extent that of *Citellus* in the narrow, short rostrum, great zygomatic breadth and general proportions. On the other hand, the dentition resembles that of *Otospermophilus,* differing only in that the teeth are much higher crowned in *C. matachicensis*. However, the high crowned dentition differs from that in *Citellus* and *Ictidomys* where the lophs, trigonids, and posterolophids are elevated as sharp lophs while in *C. matachicensis* the lophs, trigonids, and posterolophids are low and rounded and the increase in height has elevated the entire crown of the teeth. *Citellus matachicensis* appears to be most closely allied to either *Otospermophilus* or *Callospermophilus* but its exact subgeneric position is unknown. No descendants of this species are known.

Measurements

Length of skull	47.3
Width of skull at supraorbital notch	11.5

Width of skull at postorbital notch	13.3
Width of skull across posterior zygomatic root	32.0
Width of rostrum at anterior end of zygomatic plate	9.4
Length of palate	23.4
Length of diastema	11.3
Alveolar length P^3-M^3	11.0
Length of mandible	33.4
Length of diastema	6.8
Depth below M_1	6.7
Alveolar length P_4-M_3	10.5

	a-p	tr.
I	2.60	1.70
P^3	1.30	1.20
P^4	2.30	2.90
M^1	2.45	3.25
M^2	2.50	3.25
M^3	2.90	2.90
I	2.50	1.50
P_4	2.10	1.80-2.40
M_1	2.30	2.50-2.70
M_2	2.60	2.90-2.90
M_3	2.70	2.90-2.60

Citellus (Citellus?) sp.

Plate 22, figure 4

Material. A.M.N.H. No. 8338, incomplete right mandible with I and P_4-M_3.

Horizon and locality. Late Miocene or early Pliocene, "Miocene Loup Fork Formation, *Procamelus* Beds, Nebraska." Information taken from the label. Name of collector and date of collection not given.

Description. The mandible is slender with a long, shallow diastema which lies above the alveolar level at the base of the incisor. Most of the masseteric fossa is missing but anteriorly it extends forward to below the posterior half of P_4. The mental foramen is situated quite far forward at about the midpoint of the anterior portion of the ramus and just below the level of the diastema. Just behind the mental foramen there is a prominent bony knob.

The incisor is compressed, flat medially, and convex laterally. There is no trace of an anteroconid on P_4 and virtually no trigonid basin. The protoconid and metaconid form a continuous high ridge. The buccal valley is deep and bends slightly posteriorly as it passes the hypoconid. The ectolophid is low and there is no trace of a mesoconid. The talonid basin is shallow but completely enclosed. The low posterolophid passes in a gentle curve from the hypoconid around the entoconid corner to the base of the metaconid. There is no indication of an entoconid. M_1 and M_2 are compressed anteroposteriorly and are essentially identical in structure, differing only in size. There is no anteroconid present. The trigonid basins are small, shallow, and completely enclosed in the protoconid-metaconid ridge. The buccal valleys are deep and dammed by low ectolophids without mesoconids. Lingually small mesostylids are present, set off from both the metaconids and entoconids by shallow valleys. The posterolophids are low and merge into indistinct entoconids. M_3 is almost as wide as it is long with very little expansion of the hypoconid and posterolophid. The entoconid is not discernible as a distinct cusp but is submerged in the posterolophid. Neither a mesoconid nor a mesostylid is present. The metalophid is incomplete.

Discussion. This specimen bears some resemblance to the living *Citellus (C.) tridecimalineatus,* the thirteen-lined ground squirrel, and, on the basis of tooth proportions and general shape could be regarded as broadly ancestral to the more specialized ground squirrels of the *Ictidomys-Citellus* group. The protoconid-metaconid ridge is not as greatly elevated as it is in the Recent species although more so than in other contemporary forms. The anteroposterior compression of molars is greater than is generally the case in the *Otospermophilus-Callospermophilus* group or in *Ammospermophilus.* The relatively unexpanded posterior half of M_3 is also closer to the condition found in the subgenus *Citellus* than to that encountered in other ground squirrels. However, all of these characters, while very possibly suggestive of *Citellus (Citellus)* or of *C. (Ictidomys),* are still at so early a stage of development that a positive assignment to that group of ground squirrels is scarcely justified. It is most unfortunate that the age of the specimen is not precisely known; if it is early Pliocene, then the absence of more progressive contemporaneous species would tend to support the view advanced on page 238 that the subgenera *Citellus* and *Ictidomys* did not appear as such until the Hemphillian.

Measurements

Length of diastema		7.6
Alveolar length P_4-M_3		8.5
	a-p	tr.
I	2.50	1.40
P_4	1.70	1.70-2.00
M_1	1.90	2.30-2.50
M_2	2.10	2.60-2.70
M_3	2.60	2.70-2.30

CITELLUS (CITELLUS) MCKAYENSIS Shotwell

Plate 22, figure 5

Citellus (Citellus) mckayensis Shotwell, 1956, p. 728.

Type. U.O.M.N.H. F-3627, left horizontal ramus with M_1-M_3.

Hypodigm. Type and U.O.M.N.H. F-3613 and F-3659, partial mandibles without dentition.

Horizon and locality. Hemphillian, late Pliocene. East bank of McKay Reservoir, 5 miles south of Pendleton, Umatilla County, Oregon.

Diagnosis. "Molars increase in size from M_1-M_3. A species about the size of living *C. (Citellus) columbianus.* Trigonid much higher than talonid on all molars. A distinct notch is present between posterolophid and parametaconid. Metalophid connects progressively farther down on parametaconid from M_1-M_3. M_1 and M_2 are wider than long; M_3 is longer than wide." (Shotwell, 1956, p. 729.)

Description. The two edentulous mandibles are identified as *C. mckayensis* on the basis of the comparatively shallow ramus. Mandibles of *C. (Otospermophilus) wilsoni* from this locality are much deeper and in general more robust than those here referred to *C. (Citellus) mckayensis.* The diastema is relatively short and the diastemal depression extremely shallow. The mental foramen is closer to P_4 than in *C. wilsoni.* The masseteric fossa extends forward to below the posterior end of P_4.

M_1 is slightly smaller than M_2 but agrees with it in every respect except a higher and more complete metalophid. The trigonids are as well developed as in Recent species of the subgenus. The trigonid basin is enclosed on M_1 but open on M_2 and M_3. The buccal valleys of all molars are deep, broad, and closed internally by thin ectolophids; on M_3 two minor tubercles are present at the bottom of the valley. The posterolophids of M_1 and M_2 are higher than the hypoconids. A shallow lingual notch separates the metaconid and posterolophid on M_1-M_3. M_3 is elongate with an expanded posterolophid; the entoconid is not distinct, but a short lophid passes from the entoconid region towards the hypoconid.

Discussion. C. mckayensis is the earliest surely known member of the more highly specialized ground squirrels of the subgenus *Citellus*. It is considerably advanced over *Citellus (Citellus?)* sp. from the "*Procamelus* Beds" having much higher trigonid lophs. The presence of this advanced species in the late Hemphillian suggests either a somewhat longer history for the group than might have been expected, or a very rapid development of these more specialized forms during the Pliocene. I incline toward the latter view, primarily because of the absence of any advanced spermophiles in other Pliocene faunas and because of the great difference between *C. (C.) mckayensis* and *C. (Citellus?)* sp. from the early Pliocene? of Nebraska. *C. (Citellus) mckayensis* resembles *C. (Citellus) cochisei* from the early Pleistocene of Arizona and could well have been ancestral to it.

Measurements

U.O.M.N.H. No. F-3613

Length of diastema	7.5
Depth below M_1	6.6
Alveolar length P_4-M_3	12.8

		a-p	tr.
F-3627	M_1	2.00	2.70-2.70
	M_2	2.30	2.90-2.90
	M_3	3.20	3.00-2.70
F-3613	I	2.40	1.30

Ammospermophilus? sp.[1]

Plate 22, figure 6

Material. U.O.M.N.H. Nos. F-5871 and F-5763, both horizontal right rami with I, P_4-M_3.

[1] Since this paper was submitted for publication Shotwell's paper on the Juntura Basin faunas has appeared (Shotwell, J.A., et al., 1963. The Juntura Basin: Studies in Earth History and Paleoecology. Trans. Amer. Phil. Soc., n.s., v.53, pt. 1:1-77) in which a new species, *Citellus junturensis*, is described, based upon the material here referred to *Ammospermophilus?* sp. plus some additional material not seen by me. Shotwell (p. 46) points out the resemblance of *C. junturensis* to *Ammospermophilus* but does not refer his species to the latter genus because he believes the resemblances may reflect parallelism rather than direct relationship. This is, of course, possible; however, the suite of characters found in the lower dentition may reflect direct relationship to *Ammospermophilus* as I have indicated above. On the material available this relationship cannot be certainly determined but a tentative reference of this material to *Ammospermophilus* is, I believe, justified.

Horizon and locality. Clarendonian, early Pliocene. About 3 miles SW of Juntura, Oregon.

Description. The ramus is stout in relation to the size of the dentition, more so than in Recent species. The masseteric fossa terminates below the anterior end of M_1 and is pointed anteriorly. It is deeply concave with a sharp ridge bordering it below.

P_4 is much wider posteriorly than anteriorly. There is no indication of an anteroconid. A weak ectolophid closes the broad buccal valley; there is no mesoconid. The posterolophid is moderately high and curves gently forward at the entoconid corner, and the entoconid is completely submerged within it. M_{1-2} are approximately as long as wide. M_1 is smaller than M_2 but otherwise agrees closely with it. The protoconid and hypoconid are of nearly equal size. Neither an anteroconid nor mesoconid is present. The trigonid basin is enclosed anteriorly by a strong cingulum, stronger on M_1 than on M_2 in F-5871, and posteriorly by the metalophid. The degree of development of the metalophid is variable; it is stronger on M_1 than on M_2 in both specimens and more pronounced in F-5763. The posterolophids are elevated and curve gently forward at the entoconid. Small mesostylids are present on M_1 and M_2 of F-5763 but are absent on F-5871. The buccal valleys are broad and the ectolophids weak. The talonid of M_3 is expanded, with a large hypoconid, a heavy posterolophid and an enlarged entoconid area. The metalophid is weak, more so in F-5871 than in F-5763. There is a small mesostylid in F-5763 but not in F-5871. The incisors are compressed and only slightly convex laterally.

Discussion. Reference to *Ammospermophilus?* is based solely on the dentition, and because of this is open to some doubt. The diagnostic characters of *Ammospermophilus* are to be found primarily in the skull (Bryant, 1945, p. 375) and are those of a rather generalized ground squirrel. However, there are a few characters in the dentition, which, when taken together, seem to distinguish *Ammospermophilus* from *Citellus*. These are: (1) small size; (2) teeth low crowned; (3) the lack of anteroposterior compression of M_1-M_2; (4) the straight posterolophid curving only at the lingual border; (5) the equal size of the protoconids and hypoconids on M_1-M_2; (6) shallow and broad buccal valleys; and (7) the almost rectangular outline of M_3. Any one of these characters may of course be found in the subgenera of *Citellus* but I have been unable to find such a combination in any of them. *C. (Callospermophilus)* approaches the condition in *Ammospermophilus* most closely but, nevertheless, differs from it in the construction of the posterolophid, in somewhat higher crowned dentition, and in the larger size of the protoconid relative to the hypoconid on M_1-M_2. *Ammospermophilus?* sp. may therefore stand in an ancestral position for the genus. The mandible is heavier and deeper than in the Recent species but this is to be expected in any early member of the group.

Measurements

		F-5871	F-5763
Alveolar length P_4-M_3		7.00	7.10
P_4	a-p	1.30	1.35
	tr.	1.05-1.45	1.10-1.45
M_1	a-p	1.55	1.50
	tr.	1.60-1.80	1.50-1.80
M_2	a-p	1.75	1.70
	tr.	1.85-1.90	1.80-1.90
M_3	a-p	2.00	1.95
	tr.	1.95-1.90	1.90-1.85

CYNOMYS Rafinesque

Two supposed occurrences of Tertiary prairie dogs have been reported. Matthew (1899) mentioned a specimen of *Cynomys* from the Republican River of Nebraska, and this record has been repeated in later faunal lists (Matthew, 1909; Merriam, 1917; Cook and Cook, 1933; and Bryant, 1945) but I have not come across any material upon which the identification could have been based. Green (1960) has described a new species of *Cynomys, C. spispiza* (S.D.S.M. No. 57100, a mandible with P_4-M_3) from South Dakota, giving the age as either late Miocene or early Pliocene. The material was found on "the spillway of Roosevelt Lake dam, Tripp County, South Dakota" (Green 1960, p. 545), on an exposure of Valentine sand together with a ground squirrel indistinguishable from the Recent *Citellus (Citellus) richardsoni* (S.D.S.M. No. 592, a right mandible with P_4-M_1, and isolated teeth S.D.S.M. Nos. 5934-5936). The prairie dog does not appear to me to be separable from the Recent *Cynomys leucurus*. Since both species found at this locality are indistinguishable from Recent forms, I regard the age assignment as extremely questionable and suspect that the specimens were derived from Pleistocene sediments. I think it fair to state that we do not yet have unequivocal evidence of the existence of *Cynomys* prior to the Pleistocene.

The dentition of *Cynomys* is rather highly specialized being higher crowned than that known for any other North American sciurid. The skeleton is more specialized for fossorial life than that of the spermophiles, less so than that of the marmots (Bryant, 1945). I suspect that the prairie dogs did not branch off from the spermophile line before the later Pliocene.

SCIURID, *incertae sedis*

Sciurid? sp. Wilson, 1934, p. 16.
Sciurid? sp. Bryant, 1945, p. 340.

Material. L.A.C.M. (C.I.T.) No. 1513, a fragment of left mandible with P_4 and partial incisor.

Horizon and locality. Whitneyan late Oligocene. Las Posas Hills, southern part of Ventura County, California.

Description. There is some of the jaw surrounding P_4 and the barest outline of a portion of the alveolus for the incisor, but there is not enough bone present to show anything of the structure of the mandible. The metaconid on P_4 has been broken off and lost as well as some of the enamel on the posterior side of the tooth. The pattern is extremely simple with a large metaconid, protoconid and hypoconid of equal size, and no trace of an entoconid. There is no mesoconid or ectolophid. There does not appear to have been an anteroconid present. The incisor is compressed, and the enamel extends one-third of the way down the lateral side of the tooth.

Discussion. P_4 appears to be that of a sciurid but the material can tell us no more than that.

Measurements

	a-p	tr.
I	2.60	1.10
P_4	1.90	1.70-1.80

PHYLOGENETIC HISTORY

The basic question concerning the evolution of the Sciuridae is the origin of the family. Most American students would derive the Sciuridae from the Paramyidae (e.g. Bryant, 1945; Wilson, 1949b, 1960; Wood, 1955, 1959, 1962). Some European workers, on the other hand, feel that the Sciuridae, at least as regards their dentition, represent the most primitive stage in rodent evolution, and that the Paramyidae are actually more advanced (e.g. Stehlin and Schaub, 1951; Schaub, 1953, 1958; Viret, 1955). This difference of opinion is due primarily to conflicting interpretations of the anterior cusp of the trigonid. Schaub believes this cusp to be a paraconid and accordingly states (1953, p. 9) "parmi tous les Simplicidentés fossiles et récents, les Sciuridés présentent la structure la plus archaïque des molaires." Most American workers, however, interpret this cusp as a neomorph that has arisen from the anterior cingulum, and apply the term anteroconid to it. The

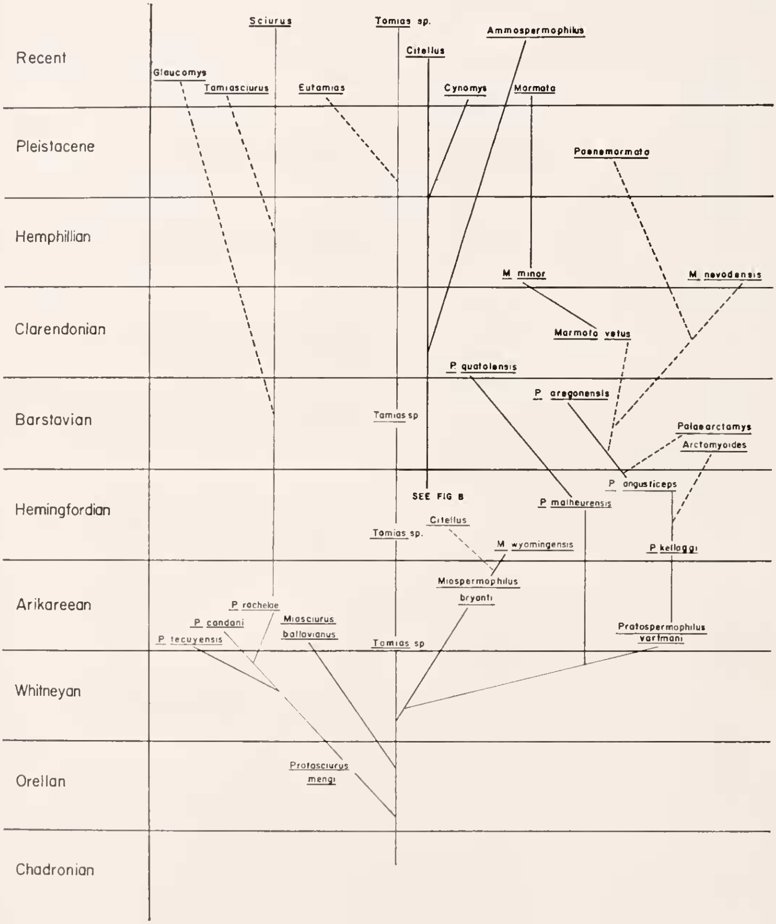

Figure 7. Phylogenetic tree of North American Sciuridae. Solid lines indicate probable relationships, broken lines possible relationships.

paraconid, they believe, was absent in the ancestral stock that gave rise to the order. The early paramyids, especially members of the most generalized subfamily, the Paramyinae, have no cusp in this position at all. This is also true of many Recent sciurids and of many of the Oligocene and early Miocene forms. There is really no concrete evidence whatever that a true paraconid was part of the rodent heritage.

It is evident, I believe, that the ancestors of the Sciuridae, and, ultimately, of all rodent groups, must be looked for within the family Paramyidae, the earliest and most primitive of rodent groups. Wood (1962, p. 116) has described the genus *Uriscus* from the late Eocene of California and believes it to be close to the actual ancestry of the Sciuridae, stating that "the pattern of the molars is so close to that of *Sciurus* that it probably could not be generically separated on tooth structure." He observes that the lower molars of this form are rhomboidal rather than rectangular, the anterior cingulum bears no cusp, the metalophid progressively shortens from M_1 to M_3 and the small trigonid basin opens posteriorly, the posterolophid curves somewhat to the entoconid, which is distinct, small mesostylids and large mesoconids are present, and the hypoconid of M_3 is expanded posteriorly. It is obvious that the dentition of this form is indeed extremely sciurid-like. The similarity ends with molar structure, however. The incisors are not compressed and the masseteric fossa ends below M_2; these characters are definitely those of a true paramyid. Whether this new form is itself directly ancestral to the Sciuridae is, of course, uncertain, but Wood's work makes it very clear that the ancestors of the Sciuridae were members of the Paramyinae.

The Paramyinae were presumably ground living forms with a rather generalized, scampering type of skeleton. In the molars, the protocones were large and the hypocones generally absent or, when present, small. Both protoconules and metaconules were present in the lophs of M^1-M^2 and the upper molars were subquadrate. The lower molars were generally rectangular but, as just mentioned, in at least one genus they were tending towards a more rhomboidal condition. No members of the Paramyinae had anteroconids on the anterior cingulum. The trigonid basins were enclosed by a metalophid posteriorly, which in some cases was incomplete. The hypoconids and entoconids were connected by marginal, somewhat elevated posterolophids. In no members of the subfamily was an entoconid crest present. In one form, *Leptotomus*, there was an indication of a forward migration of the masseter in front of the zygoma. In the mandible, the masseteric fossa ended below M_2 and the diastema was short and straight with no depression.

Just when the ancestral paramyine line reached the sciurid level of organization is at present unknown. However, the transition surely occurred in the latest Eocene or earliest Oligocene. All that was needed to complete the transition was a slight specialization in zygomasseteric structure, the dentition of certain paramyines being already almost completely sciurid-like. Once the *masseter lateralis* had migrated anterodorsally lateral to the infraorbital foramen and the masseteric fossa had shifted forward to a point beneath M_1 the sciurid level had been achieved. Sciurids were definitely present in the mid-Oligocene, and by the early Miocene several distinct lines within the family are recognizable. This would seem to indicate the existence of a rather diversified sciurid fauna in the late Oligocene with the tribal groups probably differentiating at this time. *Protosciurus mengi* of the mid-Oligocene embodies most of the features one would expect in an early sciurid, and it may well be that it is not too far removed from the earliest sciurid stock. If this is the case, an early Oligocene or, at the earliest, a late Eocene origin for the family would seem reasonable.

Several authors have suggested that the ancestry of the sciurids may be found among the Prosciurinae (e.g. Wilson, 1949b, 1960; Galbreath, 1953). Both Galbreath (1953) and Wilson (1960) have stated that *Cedromus* from the middle Oligocene of Colorado, if not a true sciurid, is at least close to the ancestry of the family. Wood (1962, p. 232) places *Cedromus* in the Prosciurinae. The infraorbital foramen and masseter in *Cedromus* and other prosciurines are completely protrogomorph with no squirrel modifications. In view of the occurrence of sciurids in the Oligocene of North America and Europe, it does not seem possible that the masseteric transition could have occurred rapidly enough for any of the known Oligocene prosciurines to have been actual ancestors of the squirrels. Quite apart from this, moreover, there is a further major obstacle to deriving squirrels from prosciurines. The real difficulty lies in the fundamental differences in the morphology of the dentition in the two groups.

All prosciurines, including *Cedromus,* have emphasized the entoconid as a discrete cusp. During the course of prosciurine history, it became progressively isolated from the posterolophid and acquired an independent crest passing into the talonid basin toward the hypoconid. Also, in almost all prosciurines, the lower molars are rectangular and considerably longer than wide. Differences between the upper dentitions of sciurids and prosciurines are less striking, but the molars of prosciurines are generally triangular, with narrow, sharply pointed protocones and rather prominent, buccally projecting mesostyles that tend to make the buccal borders of the teeth appear scalloped. Some prosciurine upper molars are much more reminiscent of those of *Haplomys* and early aplodontids in general than they are of sciurids. These characters are present throughout the history of the Prosciurinae and there is no indication of sciurid tendencies in any of the known forms within the subfamily. In view of these decided differences, I cannot see how the prosciurines can have had anything to do with the origin of the Sciuridae; the ancestry of the family is to be sought in the Paramyinae.

Bryant (1945, p. 365) and Wilson (1960, p. 64) have compiled lists of characters that they suspect were probably present in the early Oligocene sciurids. The following list agrees in most respects with theirs, differing in a few particulars.

Skull: (1) skull roof flat; (2) braincase not expanded; (3) basifacial axis only slightly bent relative to the basicranial; (4) postorbital process short and probably blunt; (5) rostrum short, relatively heavy; (6) broad interorbitally; (7) auditory bullae complete and with two septa; (8) masseter restricted to zygoma and zygomatic plate lateral to infraorbital foramen.

Mandible: (1) diastema short; (2) diastemal depression shallow; (3) masseteric fossa ending behind M_1 with no scar anterior to it; (4) well developed pocket behind M_3 for *temporalis medius* insertion.

Upper cheek teeth: (1) no hypocone; (2) posterior cingulum uniting with protocone at right angle, with slight swelling at union; (3) anterior cingulum expanded, with low parastyle; (4) metaloph and protoloph probably complete; (5) conules present but small.

Lower cheek teeth: (1) M_1-M_2 square to slightly rhomboidal; (2) M_3 elongate; (3) anterior cingulum straight, joining metaconid and protoconid; (4) anteroconid small to absent; (5) metalophid progressively shorter from M_1 to M_3; (6) trigonid basin small; (7) entoconids distinct; (8) posterolophid only slightly elevated and curved; (9) ectolophids weak and submarginal.

Incisors: (1) upper incisors broad, unfurrowed; (2) lower incisors somewhat compressed, probably unfurrowed.

Skeleton: (1) rather generalized scampering type of skeleton, without fossorial adaptations in the limbs or girdles; (2) in general the skeleton probably resembled that of *Tamias;* (3) vertebral column of moderate length with the sacrum composed of three vertebrae; (4) limbs moderately long in relation to the vertebral length, humerus and femur short in relation to the length of the radius-ulna and tibia-fibula; (5) limb bones slender and distal ends of the radius and ulna and tibia and fibula probably narrow.

Habit: forest dwelling, probably semiarboreal, as are the chipmunks and tree squirrels; seed, berry, and nut feeders.

For knowledge of the skeleton we must wait, but so far as the skull and dentition are concerned most of the characters listed above are realized in species of *Protosciurus* from the mid-Oligocene and the early Miocene and in *Miosciurus ballovianus* from the early Miocene. *P. condoni* has evolved beyond the hypothetical ancestral condition in such characters as the long, pointed postorbital process, the deep, abrupt diastemal depression, and the presence of anteroconids. However, such differences as these could have easily been acquired after the origin of the family in the latest Eocene or early Oligocene.

Early and mid-Oligocene microfaunas are well known but for the most part fail to sample forest communities. The absence of squirrels in these faunas is, therefore, not surprising if the assumption that the early members of the family were terrestrial to semiarboreal forest dwellers is accepted. If they were terrestrial and living in open country habitats, it is difficult to explain their absence in these faunas. Late Oligocene microfaunas are very poorly known and it is not surprising that we have no record of the family at that time. In view of the morphological diversity observed in the early Miocene, it is likely that the late Oligocene was a period of rather rapid diversification within the family. This diversification was no doubt profoundly influenced by the changing climatic and vegetational conditions that were taking place in both the Great Basin and Great Plains provinces.

Middle and late Tertiary floras are quite well known for the Great Basin (see Chaney, 1940, and Axelrod, 1950, 1956) but they are poorly represented in the Great Plains. Our knowledge of the vegetation of the Great Plains from the middle Oligocene through the Pliocene is limited to the Florissant flora (some elements of which are certainly plains species while the major portion of the flora indicates an upland habitat [MacGinitie, 1953]), Elias' studies (1932, 1935, 1942) on fossil grasses, and a series of rather limited florules from the Pliocene of Nebraska, Kansas and Oklahoma (Chaney and Elias, 1936).

MacGinitie (1953, pp. 57-59) has suggested that the vegetational picture for the Great Plains during the early and mid-Oligocene was one of mesic forest elements *(Fagopsis, Populus,* *Salix, Zelkova, Chamaecyparis, Sequoia, Acer, Athyana, Bursela, Carpinus, Carya, Cedrela, Dipteronia, Koelreuteria, Lindera, Osmanthus, Rhus, Robinia, Sapindus, Staphylea, Ulmus)* growing along the lake and stream borders with scrub forest and grass predominating away from the stream channels. Through the late Oligocene and the Miocene this vegetational pattern evolved towards a more open plains condition with widespread grasslands developed by the late Miocene. The forest elements were greatly reduced and progressively restricted to the stream banks. This change in the vegetational pattern was brought about by the gradual elevation of the Rocky Mountains and the consequent decrease in annual precipitation which accompanied this uplift. MacGinitie has estimated that the annual rainfall during the mid-Oligocene was near 20 inches just east of the Rocky Mountains, and it probably decreased progressively during the Miocene. By the late Miocene the Great Plains, at least south to southern Kansas and northern Oklahoma, were characterized by a semiarid grassland vegetation *(Platanus, Salix,* and *Fraxinus* along the stream borders). The southern portions of the Great Plains at this time were evidently somewhat more moist (Chaney and Elias, 1936, p. 27) with a more humid type of vegetation (including *Acer, Bumelia, Populus,* and *Ulmus)* along the stream banks.

Such evidence as there is of the Great Plains floras indicates a climate much less humid than that of the Great Basin during the Miocene. Chaney (1940) has stated that the forests of the Great Plains were displaced earlier than those of the Great Basin, with the subsequent development of widespread grassland. During the Miocene the northern Great Basin was dominated by the Arcto-Tertiary flora and a relatively temperate climate with an annual rainfall approaching 50 inches. This flora was composed of hardwood-deciduous and coniferous species. The southern Great Basin and Mohave-Sonoran areas were dominated during the Miocene by the Madro-Tertiary flora composed of live oak, conifers, arid subtropical scrub, chaparral, and plains grasslands. This vegetation was drought resistant and lived under a semiarid climate with 15 to 25 inches of rainfall annually. With the beginnings of the elevation of the Cascade and Sierra Nevada Mountains in the early Pliocene the climate changed drastically. The annual rainfall dropped some 5 to 7 inches during the early Pliocene and Madro-Tertiary floral elements moved into the northern Great Basin as the more mesic elements of the Arcto-Tertiary flora dropped out. In the southern Great Basin the semiarid shrubby species increased while the woodland elements were eliminated.

This general increase in aridity continued through the Hemphillian with a further drop in rainfall, increased temperature extremes, and absence of woodland species. Grasslands probably dominated the Great Basin during the Hemphillian, and it seems likely that the present desert areas in the Great Basin and Mohave-Sonoran areas did not develop until the Pleistocene.[1]

The development of grasslands, the compression and break-up of forest areas, and the increasing aridity must have played a major role in the history of the ground squirrels. The vegetational change could account for the almost complete absence of tree squirrels and chipmunks in the fossil record after the early Miocene.

The compression and gradual elimination of forest areas from the late Oligocene through the Miocene in the Great Plains created a series of new ecological niches while at the same time undoubtedly wiping out many habitats previously occupied by the Oligocene sciurids. This situation presumably led to strong selective pressure for adaptation to an increasingly terrestrial life, and forms capable of making the adaptive shift from forest and forest-edge habitats into the grasslands were favored. Recent chipmunks, in both their morphology and ecology, stand in an intermediate position between the tree squirrels and the ground squirrels. They are capable climbers, and will cache food in trees, but are for the most part terrestrial, living in burrows and foraging on the ground. They inhabit forest to forest-edge environments and are nut, seed, and berry eaters. I visualize the ancestral squirrels as being chipmunk-like. Such animals would be well suited to make the shift into an open grassland habitat as well as being adapted for an arboreal habit.

The transition from a forest habitat to an open plains one probably took place during the late Oligocene. Once this had taken place, several niches within the grasslands zone would be open for exploitation, and the history of the ground squirrels indeed appears to have been one of specialization within such niches.

Soon after the presumed time of appearance of ground squirrels, two distinct evolutionary lines are encountered, the spermophiles and the extinct protospermophiles (Fig. 7). Both first appear in the early Miocene, the former represented by *Miospermophilus bryanti*, the latter by *Protospermophilus vortmani*. The protospermophiles are not met with after the close of Clarendonian time.

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[1] The above account for the middle and late Tertiary climatic and floral conditions in the Great Basin has been taken primarily from Axelrod (1950).

Protospermophilus, because of its widespread distribution and association with the true spermophiles during the Miocene, is believed to be a ground squirrel which lived in the grassland areas but fed on seeds, nuts, and berries. The earliest members of this group are unfortunately poorly represented—two jaws from the John Day and a few isolated teeth from the Martin Canyon Quarry A in Colorado. At this stage, the cheek teeth have more in common with those of *Miospermophilus* than they do with those of any other early Miocene form. This would suggest that the protospermophiles and spermophiles either had a common origin or that the latter diverged from the former shortly after these had arisen from the basal sciurid stock. To the best of my knowledge, no specimens that might belong to the group have been reported from Europe or Asia. In the present state of our knowledge, it is a fair assumption that *Protospermophilus* arose in North America.

The one basic and striking trend within *Protospermophilus* is the development of a heavy, crushing dentition. From *P. vortmani* of the John Day through the Middle Miocene, *P. kelloggi* to *P. angusticeps* of the Deep River, and *P. oregonensis* of the Mascall, the lophs of the upper cheek teeth become heavier and more rounded, the lingual borders of the teeth become more massive through the development of an expanded, almost cusp-like, connection between the protocone and posterior cingulum, and there is a general increase in the overall size of the dentition. Accompanying these changes in the upper dentition, the posterolophid of the lower molars expands; the talonid basins tend to become rugose; and the mesostylid, mesoconid, and ectolophid enlarge. These changes were paralleled for the most part in the Great Basin species *P. malheurensis* and *P. quatalensis,* but in these two species there was no general increase in overall tooth size, although they were of approximately the same overall size as the plains species.

As the dentition changed so also did the zygomasseteric structure. Due to the lack of skull material for the early and mid-Miocene species, there is no way to determine the extent of the zygomatic plate in the early members of the genus. However, in view of the absence of a scar anterior to the masseteric fossa on the jaws of *P. vortmani,* it is not unlikely that the zygomatic plate was small and possibly not yet expanded onto the rostrum. This is the condition seen in the contemporary *Miosciurus* and *Protosciurus,* in which the masseteric fossa ends below M_1 with no indication of any migration of the masseter anterior to this point. By late Hemingfordian time, the masseter had moved well forward onto the rostrum. This is reflected in the anterior movement of the masseteric fossa as well as in the development of the small crescentic scar for a portion of the masseter lateralis anterior to it. Once the zygomasseteric complex had reached this stage there seems to have been little further selection for completing the sciuromorph condition. In the last known species of the genus, *P. quatalensis,* the masseteric fossa was still confluent with the ridge lateral to the incisors on the rostrum, failing to extend to the dorsal surface of the skull.

No postcranial material of *Protospermophilus* is known. The structure of the skull, however, suggests that *Protospermophilus* was terrestrial. Living arboreal forms have a much greater angle between the facial and basicranial axes of the skull and a more convex dorsal profile. In *Protospermophilus,* the skull is only moderately convex in the later forms and the basicranial axis is not bent to any degree relative to the facial. Furthermore, the abundance of these animals and of true spermophiles in deposits of stream channel and flood plain origin argues against their being arboreal.

The disappearance of *Protospermophilus* east of the Rocky Mountains after the middle Miocene may have been at least partially due to the rise of the marmots (Fig. 7) and consequent competition with them. However, it seems likely that further spread of the grassland, retreat of the forest, and removal of scattered woodland patches played a greater part in their extinction. In the Great Basin, increasing aridity and elimination of forest and scrub in that area and in the Mohave-Sonoran region during the early Pliocene were probably the major factors leading to the extinction of the group.

Miospermophilus bryanti, the first of the spermophiles, has a much more advanced zygomasseteric structure than is seen in the protospermophiles. Judging from the masseteric fossa, which is below P_4 in this species, the zygomatic plate was probably almost fully developed. *Miospermophilus* is a small ground squirrel approaching the chipmunks in size, but it differs from them and resembles the later spermophiles in having lower molars that are greatly compressed anteroposteriorly and elevated posterolophids which are rounded at the entoconid corner on M_1-M_2. *Miospermophilus wyomingensis* was undoubtedly descended from *Miospermophilus bryanti.* It is slightly more advanced than that species with smaller entoconids, higher posterolophids, and more prominent metaconules. Later Miocene and early Pliocene ground squirrels are abundant and widely distributed but are at present difficult to identify beyond the generic level. They were probably descended from *Miospermophilus* but the evolutionary sequence is hard to trace (see Fig. 8). Most of these forms are at an otospermophile level of development with low crowned teeth, low lophs, trigonids and posterolophids and rather deep mandibles. Some, such as *Citellus (O.) matthewi,* from the Snake Creek, and *C. (O.) tephrus* from Skull Springs are distinctive, but for the most part one is left with the general impression of a multitude of generalized ground squirrels differing little from locality to locality through the late Miocene and early Pliocene. By the middle Pliocene there appear to be two and possibly three distinct forms of *C. (Otospermophilus)* in the Great Basin. One is represented in the Smiths Valley, Kern River, and Thousand Creek faunas and the

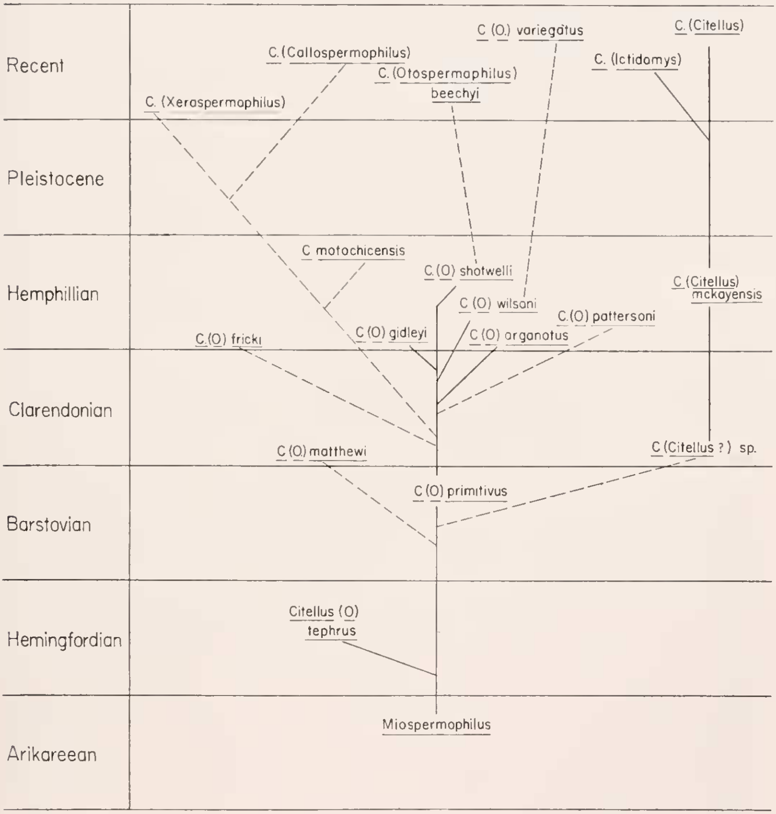

Figure 8. Relationships of subgenera and some species of *Citellus.* Solid lines indicate probable relationships, broken lines possible relationships.

other two in the northern Great Basin. One phyletic line can be traced from the early Pliocene Ellensburg fauna through *C. (Otospermophilus) wilsoni* into the late Hemphillian and may have given rise to the Recent *C. (Otospermophilus) variegatus.* The other northern Great Basin lineage is represented by several populations of *C. (Otospermophilus) shotwelli* and quite probably was ancestral to *C. (Otospermophilus) beechyi.*

Advanced spermophiles of the subgenus *Citellus* make their first appearance in the middle Pliocene. *C. (Citellus) mckayensis* is quite advanced, resembling the Recent species in most respects. (There is one mandible, A.M.N.H. No. 8338, probably of early Pliocene age, which may belong in this subgenus.) These are the only specialized spermophiles known from the Tertiary and this subgenus does not reappear in the fossil record until the early Pleistocene, in the Benson, Curtis Ranch, and Rexroad faunas. The major differentiation of the subgenera *Ictidomys* and *Citellus* would appear therefore to have been a late Pliocene and Pleistocene phenomenon. This conclusion is perhaps supported by the fact that most Recent species of the subgenera of *Citellus* intergrade into a nearly continuous sequence, indicating that differentiation is still in an active phase with no groups clearly delimited today. This fact has led some authors (e.g. Wilson, 1949c) to argue against the recognition of distinct subgenera of spermophiles in the Tertiary. However, the more advanced subgenera, *Citellus* and *Ictidomys*, were undoubtedly derived from the *Otospermophilus* group, probably splitting off in the middle Pliocene. Since this is the case, the recognition of generalized ground squirrels in the late Miocene and early Pliocene and their placement in the subgenus *Otospermophilus* is, I believe, valid.

The genus *Ammospermophilus* may have evolved by the early Pliocene but this is open to some doubt. *Ammospermophilus?* sp. from the early Pliocene of Oregon is known from only two mandibles and, although it resembles *A. leucurus* in many respects, there is not enough material available to be certain of this relationship. The fact that no other specimens referable to the genus are known from the Pliocene might indicate a later date for the origin of *Ammospermophilus.* Prairie dogs are very questionably reported from the Tertiary and it is probable that they did not arise until the late Pliocene. They were undoubtedly descended from ground squirrels of the subgenus *Citellus.*

Sometime during the middle Miocene, the marmots differentiated as a distinct group; they probably evolved from the protospermophile line, although a derivation from the true ground squirrels cannot at present be ruled out. The earliest members of the subtribe are somewhat specialized and appear to be rather far removed from *Marmota. Palaearctomys montanus* is of approximately the same size as the Recent *Marmota* but differs strikingly from it in the much smaller size of the cheek teeth and the much larger size of the incisors relative to the size of the skull. In other respects the two genera are similar and *Palaearctomys* was evidently as highly specialized for a fossorial habit as is *Marmota. Arctomyoides* is a somewhat smaller form and differs from *Palaearctomys, Paenemarmota* and *Marmota* in the shape of its lower molars. *Paenemarmota* is also rather highly specialized as regards its cheek teeth and is also only distantly related to the living marmots. *Marmota vetus* of the early Pliocene is the earliest true marmot so far recognized and was probably ancestral to *M. minor* of the middle Pliocene. The Recent species cannot be traced into the Pliocene but were very probably derived from the *M. vetus-M. minor* lineage.

Our knowledge of both tree squirrels and flying squirrels during the later Tertiary is almost nonexistent. Several species of tree squirrels are known from the early Miocene, particularly from the John Day basin. Apart from the primitive nature of the zygomasseteric structure, these species of *Protosciurus* differ surprisingly little from Recent forms. After the early Miocene, the only Tertiary record of tree squirrels consists of a fragmentary specimen from the late Hemingfordian Beatty Buttes local fauna and this, as far as it goes, appears to be completely *Sciurus*-like. No material is known that can be referred with any confidence to the flying squirrels. One mandible, Y.P.M. No. 13602, from the John Day basin has teeth that suggest those of *Glaucomys* but it cannot be placed in the group on the evidence available. In fact, it is extremely doubtful whether flying squirrels, of the *Glaucomys* group at least, could be recognized on anything less than a nearly complete skeleton. Differences between Recent *Glaucomys* and *Sciurus* in the skull, dentition and mandible are slight, and at an earlier stage of divergence they would be even less obvious.

The almost complete absence of tree squirrels, flying squirrels, and chipmunks in the fossil record is not surprising. Forest-living animals are always rare as fossils. What is surprising at first glance is the large number of squirrels known from the John Day basin and the relative abundance of tree squirrels there. However, this accords very well with the floral evidence for the early Miocene of the northern Great Basin, which indicates a region heavily forested over much of its area. Almost all other localities from which squirrels are known were presumably too far away from any large areas of forest to tap tree squirrel populations.

The history of the Sciuridae in North America has been one of short evolutionary spurts and long periods of slow change. This is particularly true for changes in the dentition. The early Miocene tree squirrels have changed remarkably little in their dentition over the last twenty million years. The spermophiles, after their origin in the late Oligocene, evolved very slowly through the Miocene and early Pliocene. The great diversification of ground squirrels is a relatively recent phenomenon that is still in progress, such forms as *Cynomys* having attained their highly specialized dentition over a short period of time, probably no longer than two to three million years. *Marmota* has evolved rather slowly since its probable origin in the late Miocene although it may have undergone a period of rather rapid evolution in the late Pliocene. While the dentition of these several groups was evolving rather rapidly over short periods of time, the zygomasseteric complex was apparently evolving at a rather slow, uniform pace throughout the Miocene and early Pliocene. The evidence reveals that the completely sciuromorph condition of the zygomatic plate was attained independently by the Tamiini, Marmotini and Sciurini. At the time, probably during the late Oligocene, when these three tribes diverged from the basal sciurid stock, the masseter was limited to the masseteric tubercle, the ventral face of the zygoma, and that portion of the anterior zygomatic root lateral to the infraorbital foramen. The masseter had not yet migrated over the infraorbital foramen and onto the rostrum. In the late Miocene, the zygomatic plate was not yet fully developed in the protospermophiles; by the early Pliocene it had reached the present level of development in the spermophiles. When it reached this level in the other lines we do not know due to lack of adequate skull material. Practically nothing can be said about changes in the postcranial skeleton of Tertiary squirrels. By the Hemphillian the spermophile skeleton was completely modern in aspect. What little skeletal material is known for the marmots is also hardly distinguishable from a Recent skeleton. In the other groups no skeletal material is known.

Just where the first squirrels differentiated is unknown. The oldest fossil recorded for the family is from the Orellan of North America but they are also known at only a slightly later date from the Stampian of France. Members of the paramyid subfamily, Paramyinae, here considered as ancestral to the Sciuridae, are known from both the Nearctic and Palearctic regions. Whatever the place of origin, a rapid dispersal, either east or west, must have occurred soon after the family differentiated from the Paramyidae, as all three sciurine tribes are present in the early Miocene of North America, and on the basis of published descriptions and illustrations, this is also true for at least two of the three tribes in Europe. There is some question as to the presence of chipmunks in the European Miocene but spermophiles and tree squirrels are certainly represented there.

Moore (1961) has recently discussed the present distribution of the Sciurinae and has concluded that the major center of dispersal for the various tribes within the Sciurinae was the Palearctic with most migrations passing from west to east across the Bering land bridge. The primary basis for this conclusion is the much greater geographic range of species of *Sciurus, Citellus,* and *Eutamias* in the Palearctic than in the Nearctic and the assumption that dominant species of mammals occupy the largest ranges and can expand their ranges most effectively. This is probably generally true but the present ranges of *Sciurus vulgaris, Citellus undulatus,* and *Eutamias sibiricus* in the Palearctic can be interpreted in a different manner. Moore (*op. cit.,* p. 9) considers the effect of Pleistocene glaciation on the ranges of these species and points out, quite correctly I believe, that each species could have retreated to refugia in Europe and China during the maximum glacial advance and then migrated back into their present extensive ranges as the glacial ice sheets retreated. The present range, then, may merely represent a reoccupation of large areas where no other species were present to offer competition.

During the late Pleistocene there is evidence (Hopkins, 1959) that there was no forest cover across the Bering land bridge. This would have made it almost impossible for species of *Sciurus* to migrate in either direction and left the present range of *S. vulgaris* in the Palearctic completely vacant and open to reoccupation without competition from other members of the genus. Species of *Eutamias* might possibly have been able to cross this bridge but chipmunks generally require at least scrub trees in their habitat. Consequently, here too, the large range now occupied by *E. sibiricus* would have been uncontested. Only species of *Citellus* and *Marmota* could have migrated across the Bering land bridge with any ease and it is only in these two genera that we find more than one species now living in the Palearctic. Therefore, it would appear to me quite possible that the large range of *S. vulgaris* and *E. sibiricus* merely represents a recent occupation of large areas where they were not faced with competition and that their present distribution does not *per se* qualify them as dominant species and, hence, as species which could expand from their ranges most effectively from the Palearctic eastward into the Nearctic. The present distribution of *Eutamias sibiricus* may have resulted from migration west across the Bering land bridge rather than from expansion from a refugium in northeastern China as Moore suggests.

The same dispersal pattern, west to east, would seem even more probable for *Citellus* and *Marmota*. *Citellus undulatus* is found today in both the Nearctic and Palearctic and its present range in Eurasia could be interpreted as resulting from migration west across the Bering land bridge during the Pleistocene as could the occurrence of the other species of *Citellus* in the Palearctic. The major radiation of the ground squirrels certainly appears to have taken place in the New World. Of the twenty-nine Recent species of *Citellus* (from Moore, 1961, p. 4), twenty-three are found in the Nearctic, plus the genera *Ammospermophilus* and *Cynomys,* and five species of *Marmota* occur in the Nearctic while three are found in the Palearctic. On present evidence, migration from this area of major radiation into the Palearctic would seem at least as plausible as the migrations from west to east suggested by Moore.

REMARKS ON OLD WORLD TERTIARY SCIURIDS

Any discussion of the evolution and dispersal of the various phyla within the family Sciuridae, based solely on the fossil record in North America, is, of course, incomplete. Interpretations as to the place and time of origin of certain phyletic lines within the family suffer from a lack of familiarity with the Old World record and this difficulty is compounded by the difference in approach of European and American workers who have dealt with sciurid material. The true relationships of many European species are obscured by a tendency to assign all material to *Sciurus*. Only a complete review of all the Old World fossils can hope to straighten out this confusion and lead to an integration of our knowledge of the family as a whole. A further complication is the lack of a fossil record for various groups that are numerous and widespread in the tropics today.

Among the Tertiary species described by European workers, there are several assigned to the genus *Sciurus* that appear to be more closely related to the spermophiles than to the tree squirrels. Among these are *S. feignouxi, S. fissurae* and *S. bredai*. Wilson (1960, p. 60) has pointed out the similarity of these species to

Miospermophilus bryanti. In general, as in *M. bryanti,* the mandibles appear to be slender, the diastemal depressions shallow, and the entoconids partially or completely submerged in the posterolophids in these species.

From at least the earliest Miocene to the present, the evidence quite clearly indicates the presence of tree squirrels, chipmunks, and ground squirrels in North America and it is becoming clear that this is true for Europe also. It seems likely that the more specialized forms found today in the Oriental, African and tropical American regions are the result of invasions into areas offering greater possibilities for diversification than are to be found in the Holarctic region. These invasions must have occurred at several different times during the history of the family, those into Africa probably occurring at a relatively early date and that from Central into South America only at the end of the Tertiary. Unfortunately, there is only one Tertiary record for the family in Africa (Lavocat, 1956b), and no record in Central America; the only Asian Tertiary sciurids reported (Bohlin, 1946) are much too fragmentary to allow of accurate generic determination.

Dehm (1950) has described *Paracitellus,* from the Burdigalian of Germany and placed it in the Sciuridae. From his illustrations and description it seems evident that *Paracitellus* is not a sciurid. The lower molars are much longer than they are wide, the few upper cheek teeth known show a rather complicated arrangement of lophs with a crest passing from the protocone between the protoconule and metaconule, and the masseteric fossa ends below M_2-M_3. These characters indicate a much closer relationship to the paramyids, particularly to the prosciurines, than to the Sciuridae.

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